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Chewing and Sucking Lice as Parasites of Mammals and Birds

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ABSTRACT

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In all stages of their development, about 2,500 species of chewing lice are parasites of mammals or birds. More than 500 species of blood-sucking lice attack only mammals. This publication emphasizes the most frequently seen genera and species of these lice, including geographic distribution, life history, habitats, ecology, host-parasite relationships, and economic importance. Information is given on modern methods of control of these lice on domestic animals, small animals, poultry, and humans, as well as a historical review of earlier methods of louse control. Also included is a historical review of the scientific classification of these lice, including some of the disagreement between various taxonomists. This publication should be a primary reference for medical and veterinary entomologists, livestock managers, extension specialists, domestic-animal researchers, and veterinarians.

Keywords: chewing lice, sucking lice, Mallophaga, Anoplura, Menoponidae, Philopteridae, Trichodectidae, shortnosed cattle louse, human lice, louse control

While supplies last, single copies of this publication may be obtained at no cost from Dr. O.H. Graham, USDA–ARS, P.O. Box 969, Mission, TX 78572. Copies of this publication may be purchased from the National Technical Information Service, 5285 Port Royal Road, Springfield, VA 22161.

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PREFACE

Years ago, Manning Price and I began writing a book about livestock insects. After slowly learning about book writing and making some mistakes, we did write the book. But we were never able to complete all the chapters in a particular year. Manning, with little or no help from me, wrote the chapter on livestock lice, and that chapter was in the hands of an ARS editor at the time of his death.

Although I had only the fuzziest acquaintance with lice, I undertook the task of putting that chapter into final form—gathering up his collection of books, bulletins, reprints, etc., and then indexing and filing them in alphabetical order. (Manning didn't use index cards. He had an intimate acquaintance with his collection of publications and could pull any particular one out of the stack on his desk at any time.) My tasks of learning something about lice and organizing the literature certainly delayed the issuance of this book.

At about the same time, it was decided that the original plan to publish a single book at this level of detail—and keep it up to date—was impractical. So we are publishing one group of insects at a time. This publication is the first.

So now you know how I came to write with all the authority I could muster about all the crawly little critters that I had never really wanted to learn about. Inevitably, I did become interested in them, but if you find mistakes—and I'm sure that any very discerning reader will—they are *my* mistakes, not Manning's. All I could do was try to remain faithful to his concept of what people might want to know about lice—or perhaps it was his concept of what people *ought* to know about lice.

This project of writing a book about livestock insects faltered and would certainly have failed except for the guidance and support of many ARS and Texas A&M University management-type people. To name only a few, there was T.W. Edminster, who first approved "Livestock Insects" for publication by ARS. And Rex Johnston, Claude Schmidt, Bob Hoffman, and Roger Drummond provided ample support through the years.

The people from ARS Information Staff labored with us from that beginning long ago. Junith Van Deusen in particular has been the patient and persevering editor on this project.

Gathering illustrations was an important part of book writing, and numerous people have helped with that. But we specifically mention Sam Wen Wang and Jan Read at College Station, TX, and Rene Davis of ARS at Weslaco, TX.

As for secretarial help, we were assisted by several excellent and dedicated workers. Elizabeth Ann Andrus of Texas A&M University and Suzanne Thomas, Doris Ernst, and Virginia Moffitt of ARS were outstanding assistants who must have privately grieved about our bookwriting skills and deplored the slow pace at which we worked.

Insect taxonomists are not in complete agreement on the scientific classification of the small, wingless, parasitic insects that are commonly known by the Old English word "lice." Apparently Packard (1887) was the first to suggest that parasitic lice are related to the free-living booklice or barklice (= psocids) (order Psocoptera). Kellogg (1896, 1902), a prominent early specialist in the classification of lice, agreed. It is now generally accepted that both chewing and sucking lice descended from psocidlike ancestors, and some entomologists have even placed all orders in the superorder Psocodea. The development of the parasitic habit by Mallophaga and Anoplura was explained by Osborn (1891) as having been a progression from the free-living state to a semiparasitic form that sometimes fed on both plants and vertebrate hosts to the modern parasite. Symmons (1952), who studied the heads of both booklice and parasitic lice, found that the tentorium (internal skeleton of the head) was well developed in Psocoptera and was reduced or absent in parasitic lice (fig. 1). She concluded, and more recent authors have agreed, that in the course of evolution the tentorium was progressively reduced in size and that the phylogenetic order of the groups is Psocoptera, Amblycera, Ischnocera, Rhynchophthirina, and Anoplura.

Agreement on the phylogeny of the chewing and sucking lice has not been followed by agreement on group names for them or on the relation of the subgroups to each other. Leach (1815) placed all parasitic lice in the order Anoplura, but Nitzsch (1818) soon applied the name Mallophaga to the chewing or mandibulate lice. Latreille (1825) recognized the existence of two groups of parasitic lice—chewing and sucking—but he gave them names that were never adopted by other workers. Ewing (1929) and Ferris (1931, 1951) affirmed Anoplura and Mallophaga as orders, with Amblycera and Ischnocera as suborders of Mallophaga. Ferris (1931) established Rhynchophthirina as a third suborder of Mallophaga to accommodate an unusual species: the elephant louse (*Haematomyzus elephantis*). Since 1931 most American workers have used Ferris's classification, but Europeans have usually used other arrangements. Jeu et al. (1990) argued that Rhynchophthirina differed from other Mallophaga sufficiently to justify placing *Haematomyzus* in a separate order, for which they proposed the name Rhynchophthiraptera.

Hopkins (1949) was convinced of the close kinship of chewing lice and sucking lice and decided that Ferris' recognition of Mallophaga and Anoplura as insect orders was not justified. Instead, he followed Haeckel (1896) and Weber (1938b, 1939), who had placed all parasitic lice in a single order: the Phthiraptera. On the basis of broadened studies that added other morphological characteristics to the usual classification based on mouthparts, Königsmann (1960) and Clay (1970) added their support to Hopkins' placement of all parasitic lice in a single order. However, they believed that Hopkins' suborder Mallophaga combined groups that are not close kin and that use of the name Mallophaga should be discontinued. The two classifications of Phthiraptera are compared below:

Hopkins (1949)	**Clay (1970)**
Order Phthiraptera	Order Phthiraptera
Suborder Mallophaga	
Superfamily Amblycera	Suborder Amblycera
Superfamily Ischnocera	Suborder Ischnocera
Superfamily Rhynchophthirina	Suborder Rhynchophthirina
Suborder Anoplura	Suborder Anoplura

The heads of representatives of Clay's four suborders are illustrated in figure 2.

After a thorough study of the characteristics and phylogenetic relationships of the five higher taxa in their superorder Psocodea (Psocoptera, Amblycera, Ischnocera, Rhynchophthirina, and Anoplura), Kim and Ludwig (1978b) agreed with the widely held opinion that modern taxa are derived from a common ancestral stock. They went on to hypothesize that primitive ancestors of today's parasitic lice invaded new habitats (animal skin and deposits of skin debris) in geologic times and gradually adapted to a parasitic existence. Kim and Ludwig supported the belief that Amblycera are the most primitive of the parasitic lice and that Ischnocera and Rhynchophthiri na evolved later. However, they rejected the opinion (Clay 1970) that Anoplura were derived from Ischnocera and suggested that Anoplura arose from a single ancestor—a primitive psocodean—and that similarities between Anoplura and Mallophaga are the result of parallel evolution that occurred because of similar habitats and adaptive roles. Haub (1980) disagreed with Kim and Ludwig and argued in support of Königsmann (1960) and Clay (1970), who had placed all parasitic lice in the order Phthiraptera. In response, Kim and Ludwig (1982) restudied the question but ended by retaining the classification they had proposed in 1978.

Future availability of fossil forms of Psocodea, or other evidence, may some day bring about full acceptance of the views of Haub (1980) and of others whom he supported. But a departure at this time from the classification used by most American entomologists [for example, Kim and Ludwig (1978a) and Emerson and Price (1981)] would serve no useful purpose. Therefore, we use two ordinal names for the parasitic lice: Mallophaga for the chewing lice and Anoplura for the sucking lice.

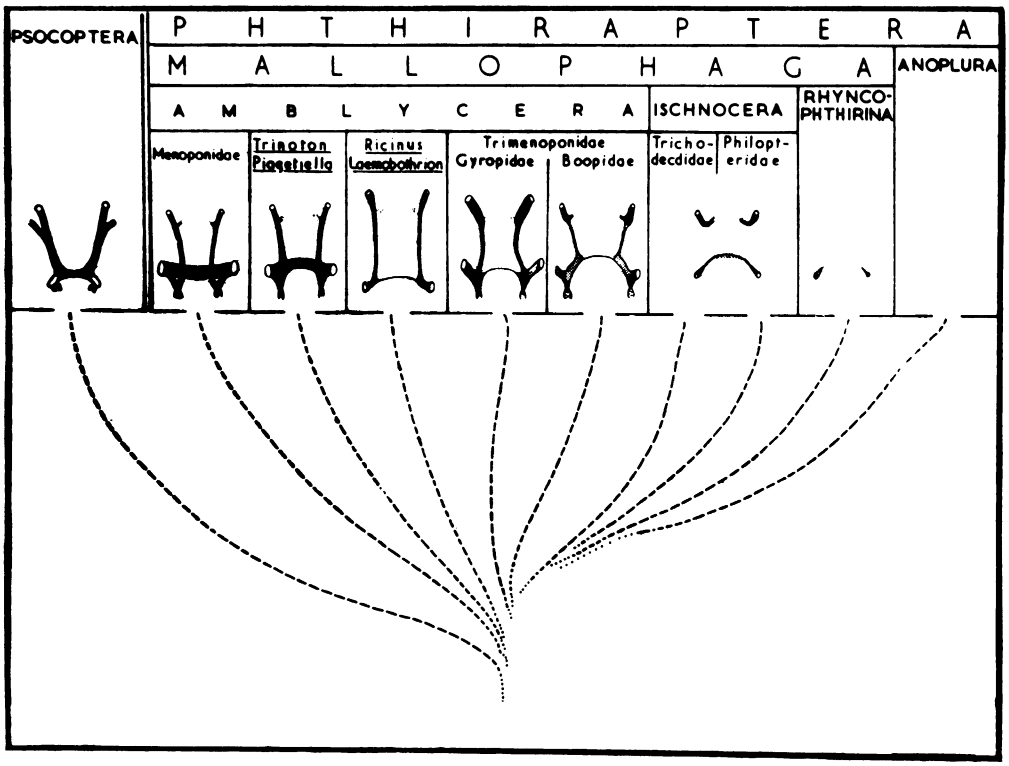


Figure 1. Size and shape of tentorium in Psocoptera, Mallophaga, and Anoplura. From Symmons (1952), reprinted by permission of Academic Press Ltd, London.

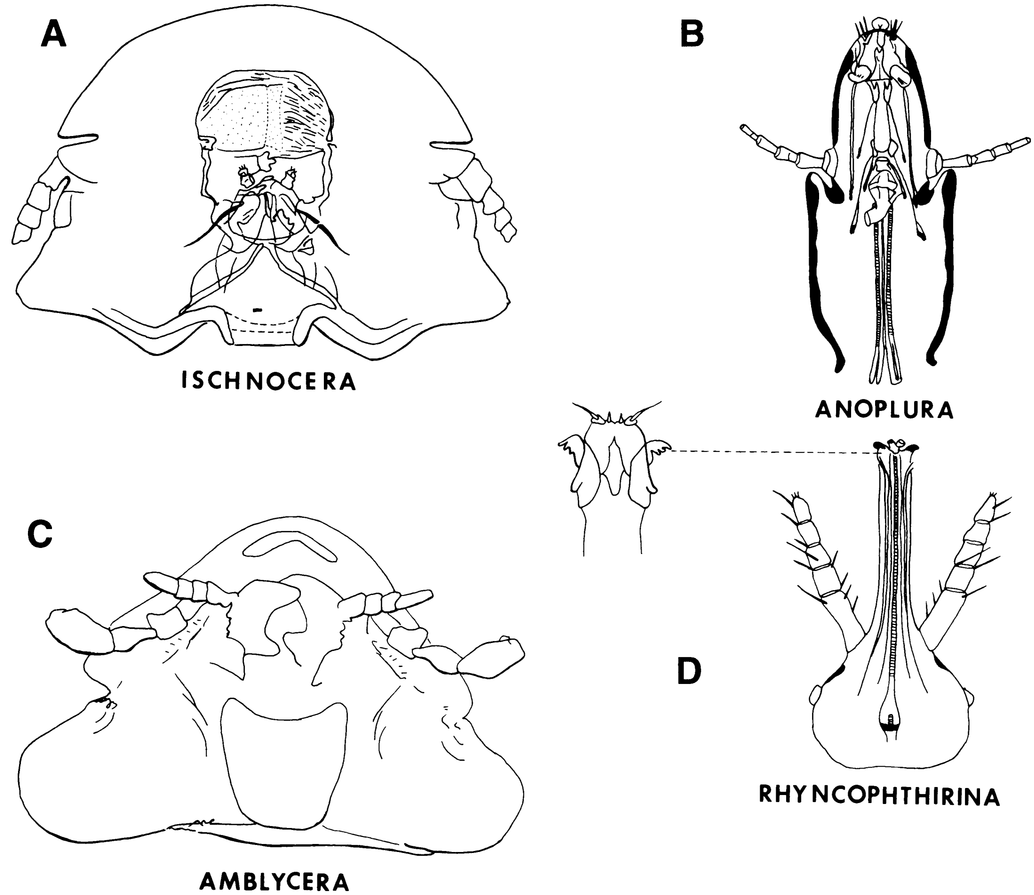


Figure 2. Outline of head in three major groups of Mallophaga (suborders Amblycera, Ischnocera, and Rhynchophthirina) and in Anoplura. Redrawn with minor modification by Jan Read as follows: ***A***, From Clay (1938b), courtesy of American Museum of Natural History; ***B*** and ***D***, from Ferris (1931), courtesy of Cambridge University Press; ***C***, from Bedford (1932b), reprinted by permission of Onderstepoort Veterinary Institute, South Africa.

R.D. Price, however, has changed his views on the classification of lice. In papers published after 1992, he has used the European name, Phthiraptera, as an ordinal name for both the chewing lice and the sucking lice (Clayton et al. 1992, Price and Clayton 1993).

All lice in the orders Mallophaga and Anoplura are obligatory parasites of birds or mammals and, as such, are totally dependent on their hosts for food and for the microhabitat they must occupy to survive. Smit (1972), as cited by Moreby (1978), coined the word "dermecos" for the microhabitat of lice, the microenvironment created by the host skin and its outgrowths. Rozsa (1991) concluded that the ancestors of Mallophaga and Anoplura were all free-living species before the Triassic period and did not parasitize the skin of ancient reptiles.

Murray (1987) discussed the hair coat of mammals and its modifications—such as wool and fur—as an environment for chewing and sucking lice. Most mammals and birds regulate the number of lice that they tolerate (which is usually quite low) by self-grooming. Whether it is by rubbing and scratching (of a mammal) or by preening (of a bird), the normal host in a good state of health manages to remove most of its lice from its body (Murray 1990).

All stages of development of lice are found on the host, and individual lice soon die if they are lost from their host. The stages are the egg, three nymphal instars each marked by a molt of the exoskeleton, and adult. Because nymphs closely resemble adults (fig. 3), metamorphosis is simple (gradual).

Lice tend to be highly host specific; that is, usually a louse species can parasitize only a single animal species or a small group of closely related animal species (Kim and Ludwig 1978a, Emerson and Price 1985,). In a study of Neotropical bird lice in which 127 species of birds were collected, Clayton et al. (1992) obtained evidence that the lice were extremely host specific. However, Price and Clayton (1993) suggested that other species of lice are less likely to be restricted to a single host than was once thought. Many early taxonomists incorrectly assumed that lice collected from different species of hosts must themselves be different species, and some of their species have been placed in synonymy.

Many species of mammals and birds are sometimes injured by lice. Large numbers of lice cause irritation, inflammation, and pruritis by crawling about on the skin and by their feeding activity (Sosna and Medleau 1992a). Besides serving as disease vectors, lice can provoke a number of direct host injuries. Hopla (1982) and Hopla et al. (1994) stated that lice can cause anemia, detrimental immune reactions (hypersensitivity, anaphylaxis, etc.), irritability, dermatitis, skin necrosis, reduced weight gains, secondary infections, localized hemorrhages, blockage of orifices (such as ear canal), inoculation of toxins, and exsanguination.

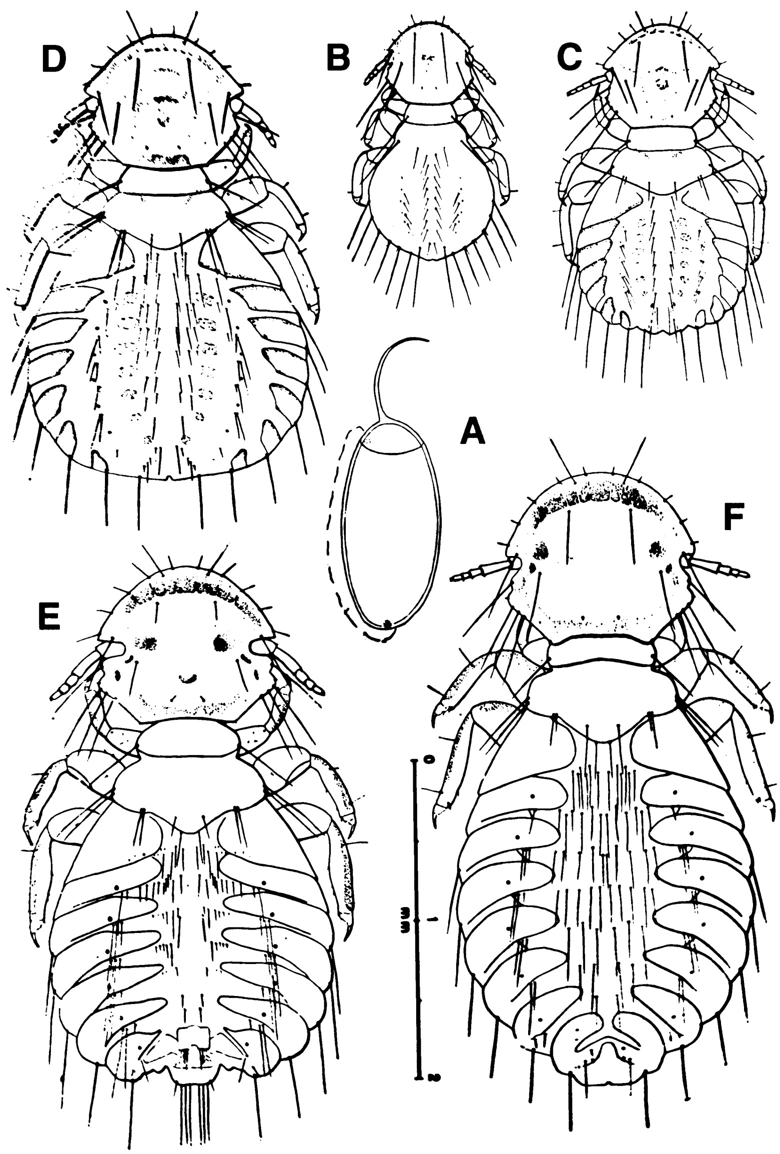


Figure 3. Life stages of *Goniodes gigas* (large chicken louse). ***A***, Egg; ***B***, first-instar nymph; ***C*,** second-instar nymph; ***D***, third-instar nymph; ***E***, adult male; ***F***, adult female. All drawn to same scale. From Conci (1956), reprinted by permission of Societa Entomologica Italiana.

ORDER MALLOPHAGA (CHEWING LICE)

All mandibulate, or chewing lice, are in the order Mallophaga. Most species have prominent mandibles on the underside of a head that is bluntly rounded and wider than the thorax. However, a few lice in the family Ricinidae have mouthparts that are modified to pierce the host's skin (see *B* in fig. 28). Although the tentorium lacks dorsal arms and is variable in size and completeness of development, the tentorium is present in all Mallophaga (Symmons 1952, Kim and Ludwig 1982). The prothorax is distinctly separated from other thoracic segments.

Of the approximately 2,500 species of Mallophaga, it is estimated that more than 2,000 are parasites of birds and that only 467 are parasites of mammals (Kim et al. 1990). The North American fauna consists of 1,005 species and subspecies, of which 903 species and subspecies are from birds. The larger number of bird feeders has caused some writers to refer to Mallophaga as bird lice, but "chewing lice" is more descriptive of the order as a whole.

Each of the two large suborders, Amblycera and Ischnocera, contains families whose species parasitize birds and other families whose species parasitize mammals. But within a family, with rare exceptions, all of the species are parasites of either birds or mammals. Regardless of whether its host is a bird or a mammal, a chewing louse passes its entire life in a very specialized microhabitat on or near the host's skin and feeds on the organic substances encountered in that habitat: particles of skin, hair, feathers, or fur; other skin debris (sometimes called scurf); dried tissue fluids; and in some instances, blood.

In general, mallophagans change hosts when two or more mammals or birds of the same species are in close contact with each other, such as the contact between a female and her young. But Keirans (1975a, b) recorded the frequent collection of keds (hippoboscid flies) or other flying insects with lice firmly attached to them (fig. 4). It is presumed that the louse is using the fly for transport from one host to another (= phoresy). This means of movement to a new host is apparently used by both Mallophaga and Anoplura and by both bird lice and lice of mammals.

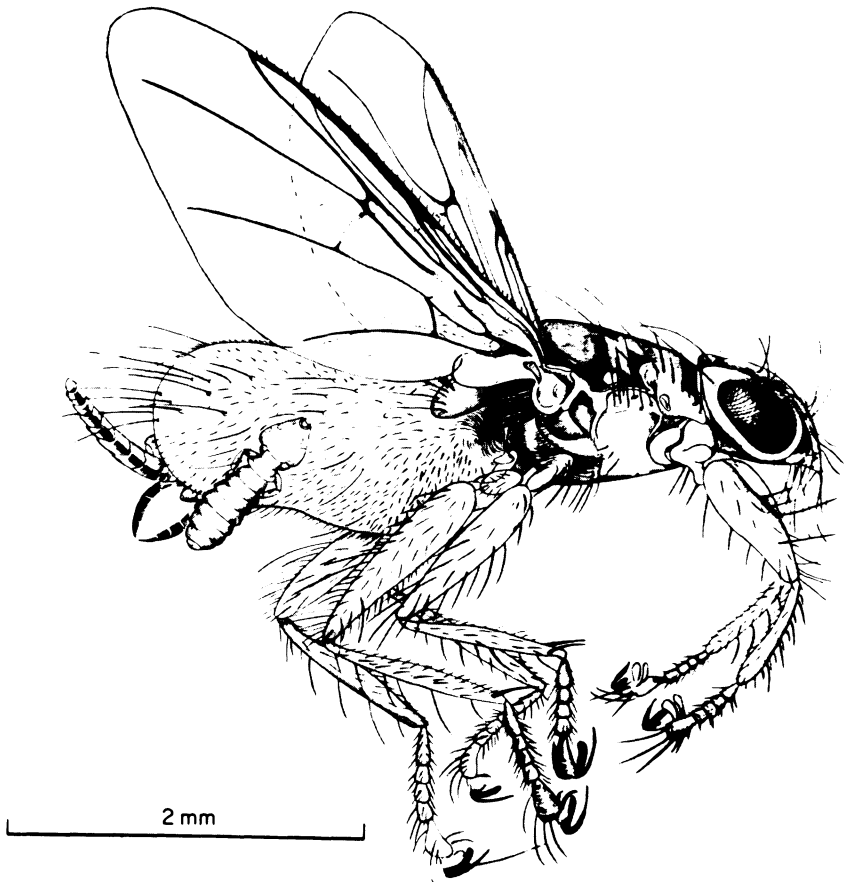


Figure 4. Example of phoresy: A mallophagan is attached to abdomen of a hippoboscid fly. From Askew (1971), reprinted by permission of author.

SUBORDER AMBLYCERA

Chewing lice in the suborder Amblycera differ from other Mallophaga in that the third antennal segment is pedunculate and the antennae are recessed in grooves on the head (fig. 5); the mandibles lie parallel to the ventral surface of the head and cut in a horizontal plane; the maxillary palpi, which usually have four joints but may have two to five joints, are present; and usually a distinct suture divides the mesothorax and metathorax. Labial palpi are present in all families except Ricinidae. The tentorium is complete except that it lacks dorsal arms (see fig. 1).

Authorities such as Clay (1949b) agreed that the Amblycera are closer in their habits and morphological characters to their free-living, psocidlike ancestors than are other Mallophaga. The species from mammals are found only on the more primitive living mammals (Emerson and Price 1985). The 836 known species of the suborder were for many years distributed into 6 families, but Emerson and Price (1976) established a seventh, the Abrocomophagidae, to accommodate a new, distinctly different species.

Amblycera in four of the families parasitize mammals, and those in the other three parasitize birds. But there are rare exceptions; for example, a species of Boopiidae is a parasite of cassowaries (Clay 1971). Although the Amblycera feed on particulate materials from the host's skin and its covering, some of its members are known to occasionally ingest blood, and others are believed to feed on blood frequently or perhaps entirely.

FAMILY ABROCOMOPHAGIDAE

The family Abrocomophagidae was erected by Emerson and Price (1976) for a new genus and species of Amblycera, *Abrocomophaga chilensis,* from a rat chinchilla (*Abrocoma bennetti*) that is found in Chile. The monotypic family is distinguished from other Amblycera by having a single unmodified tarsal claw on each leg and only five pair of abdominal spiracles.

A. chilensis is a small, slender louse whose life history and host-parasite relationships are unknown.

FAMILY BOOPIIDAE

The Boopiidae[1] are a relatively small group of chewing lice that parasitize Australasian marsupials (two exceptions are known). The head of these lice has two long, stout, backward-pointing, spinelike processes (fig. 6). The lice are distinguished by the presence of a usually spiniform seta on a protuberance on each side of the mesonotum. In addition, tergum 1 is fused with the metanotum, and the gonapophyses are distinctive (Clay 1970). Boopiidae have two claws at the end of the tarsus whereas the Trichodectidae—many of which infest domestic animals—have only one claw (Kettle 1984). Insemination by Boopiidae is acomplished by the transfer of a spermatophore to the female by the male (Kéler 1971).

Since Kéler (1971) revised Boopiidae, a new genus and additional species have been described (Clay 1971, 1972, 1976) and 8 genera and 40 species are now recognized. All are parasites of marsupials in Australia and New Guinea except *Therodoxus oweni* from a cassowary in New Guinea (Clay 1971) and *Heterodoxus spiniger,* a louse that infests dogs worldwide. The exceptional occurrence of a single species of Boopiidae, *T. oweni*, on a bird is difficult to rationalize. Clay postulated that the cassowary may have recently acquired the louse from a marsupial or may have long ago acquired an ancestral form that adapted to the cassowary and evolved into the modern species. Or as Clay (1970) had previously suggested, prehistoric marsupials may have acquired their Mallophaga from birds and *T. oweni* may be a direct descendant of that ancestral stock.

Genus *Heterodoxus*

Kéler (1971) listed 13 species of *Heterodoxus,* of which 7 were newly described by him. Except for *H. spiniger,* all are parasites of wallabies and kangaroos in Australia and New Guinea. Rock wallabies (*Peterogale* spp.) are infested with two species of *Heterodoxus*: *H. octoseriatus* and *H. ampullatus.* The *H. octoseriatus* group contains eight previously described species and three others described by Barker (1991a). The phylogeny of the *Heterodoxus octoseriatus* group was inferred by Barker (1991b), who decided that two character states support a thesis of monophylety.

Heterodoxus spiniger

Although it was sometimes referred to as the kangaroo louse, *Heterodoxus spiniger* (figs. 7–9) was described by Enderlein (1909) from specimens from a dog in southern Africa. For many years it was often confused in the literature with *Heterodoxus longitarsus* and sometimes with other species (Plomley 1940, Kéler 1971). Werneck (1941) ended the confusion by stating that the only confirmed host of *H. longitarsus* is the red-necked wallaby (*Wallabia rufogrisea*). And it is now believed that *H. spiniger,* like other Boopiidae, was originally a

[1]This spelling was used by Mjöberg (1910) when he established the family, but it later became fashionable to use the spelling "Boopidae" [see comments of Clay (1971)]. Kéler (1971) restored the original spelling, and later authors such as Clay (1976) and Emerson and Price (1985) referred to the family as Boopiidae.

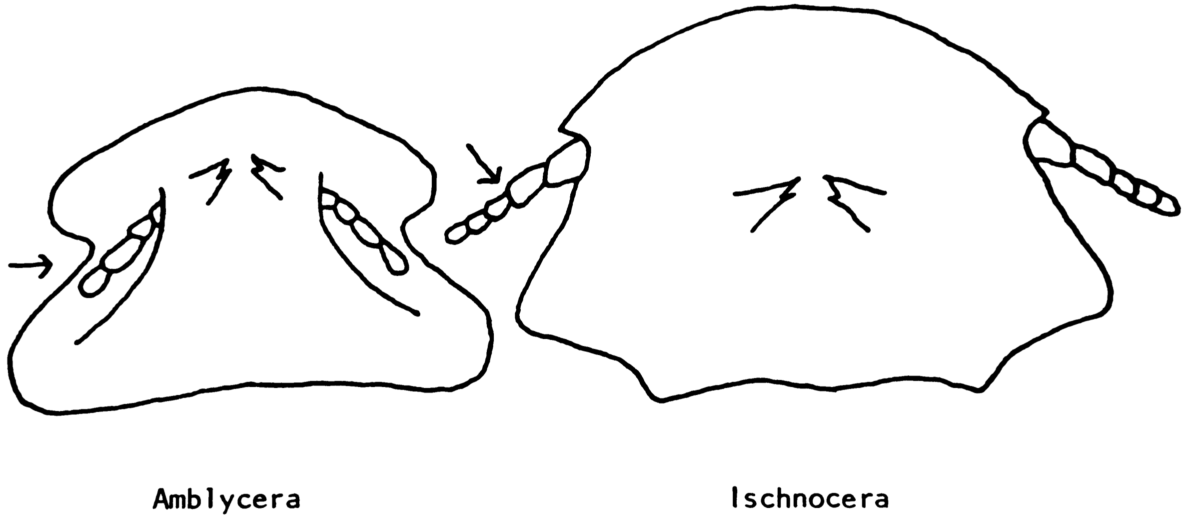


Figure 5. Separation of Amblycera and Ischnocera. Note that in Amblycera the antennae are either clubbed or capitate and are concealed in a groove on underside of head. From Tuff (1977), reprinted by permission of Texas Journal of Science.

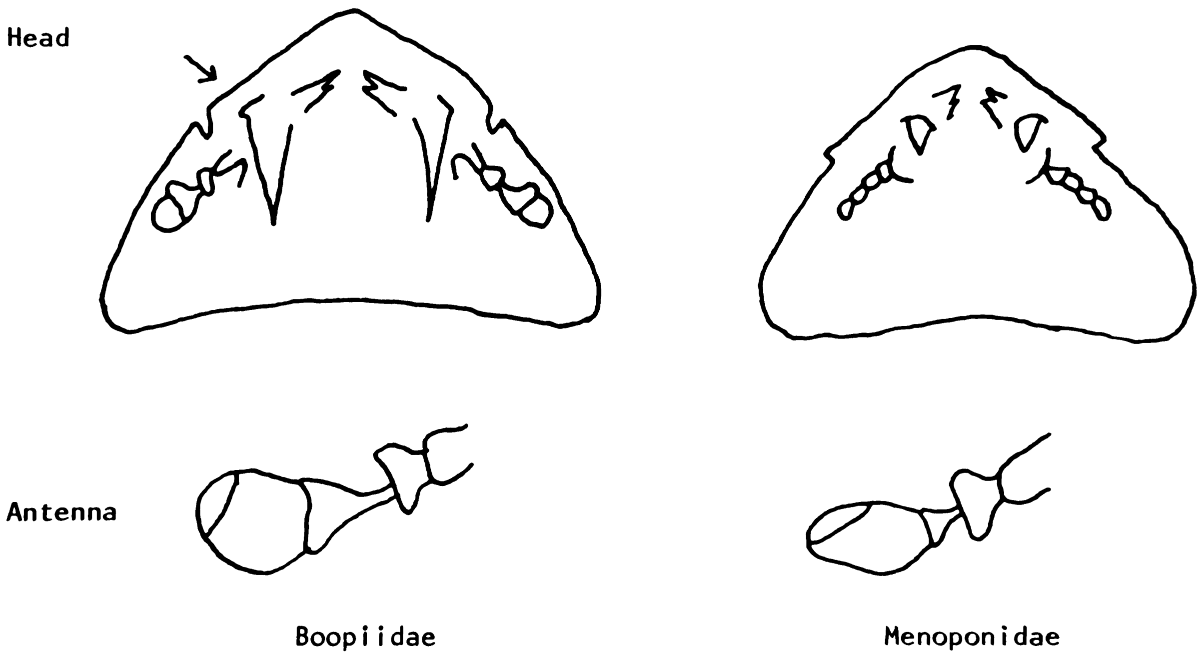


Figure 6. Separation of Boopiidae and Menoponidae. Note that Boopiidae have two long, stout, backward-projecting, spinelike processes on underside of head and that the antennae are clubbed. From Tuff (1977), reprinted by permission of Texas Journal of Science.

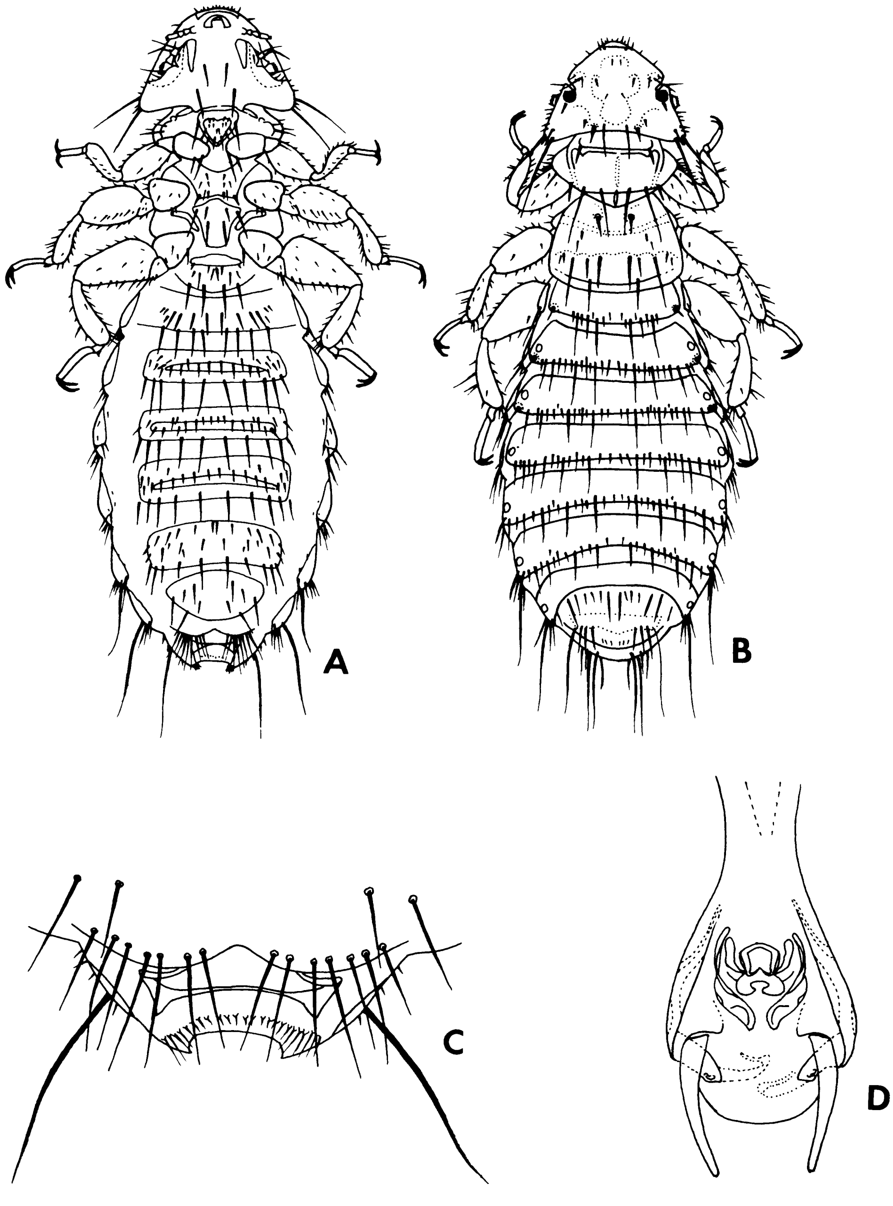


Figure 7. *Heterodoxus spiniger*: ***A***, Ventral view of female; ***B***, dorsal view of male; ***C***, female terminalia; ***D***, male genitalia. Redrawn with minor modification by Jan Read from Emerson and Price (1975); courtesy of Brigham Young University Science Bulletin, Biological Series.

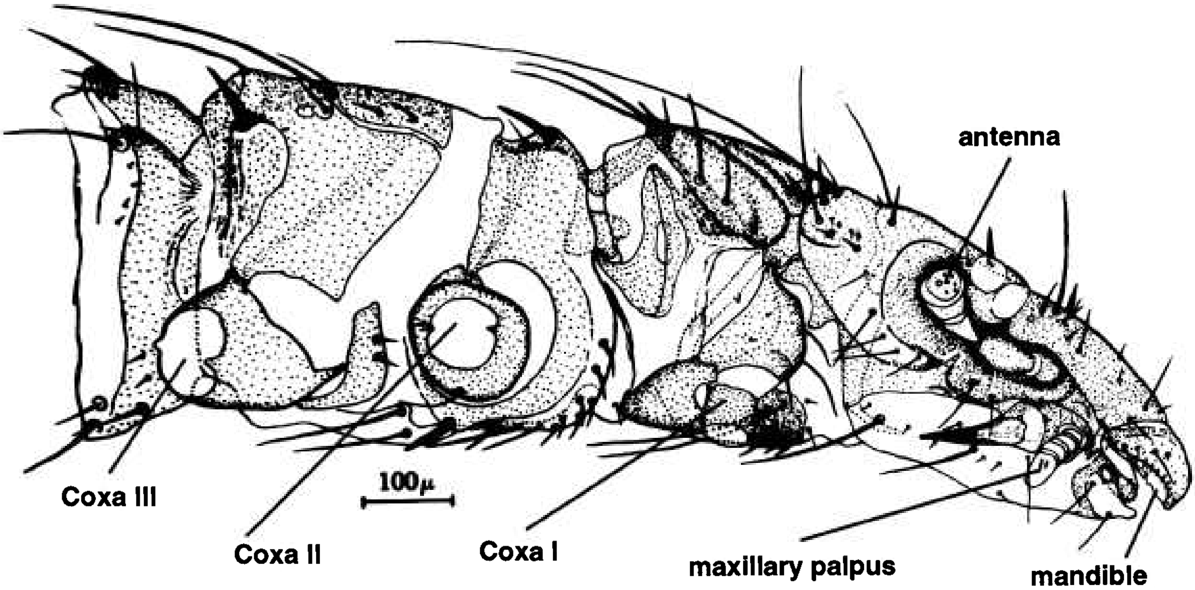


Figure 8. *Heterodoxus spiniger.* Side view of head and thorax. From Kéler (1971), reprinted by permission of Australian Journal of Zoology.

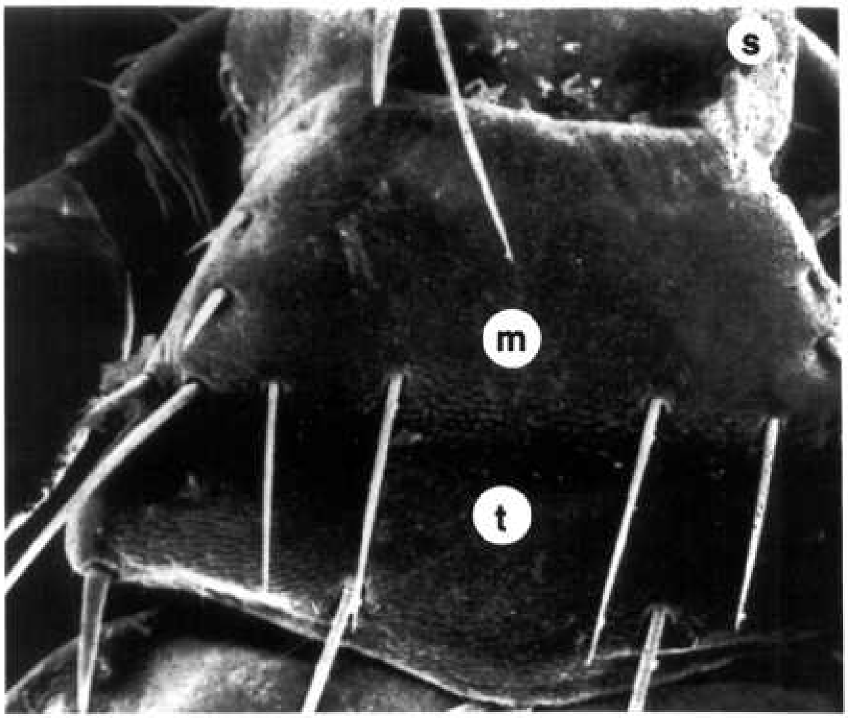


Figure 9. *Heterodoxus spiniger.* Dorsal view of thorax and first two abdominal segments. Note seta (**s**) borne on protuberance on side of mesonotum; metanotum (**m**) and tergum 1 (**t**) are also shown. SEM × 140. From Clay (1970), reprinted by permission of publisher. © British Museum (Natural History), 1970.

parasite of marsupials in Australasia but that it transferred to the dingo and then, in modern times, to the domestic dog (Murray and Calaby 1971, Emerson and Price 1985).

Although *H. spiniger* is more prevalent in tropical and temperate regions than in cold climates, it has been recorded from all continents except Europe and Antarctica. Nelson (1962) noted that it had not been reported from northern North America. Within climatically favorable regions, its distribution is believed to approximate that of its principal host, the domestic dog.

Apparently the life history and behavior of *H. spiniger* have not been described.

Heterodoxus spiniger is best known from domestic dogs, but it also parasitizes other Canidae (see appendix A). In addition, it has been reported from two species of wallaby: *Wallabia agilis* (Kéler 1971) and *W. bicolor* (Plomley 1940). But Emerson and Price (1981) did not recognize those records or the records of *H. spiniger* from Geoffroy's cat (they listed other species of *Heterodoxus* from the two wallabies). Reports of collections from a raven, a crow, and a human are probably invalid.

Apparently the effects of *H. spiniger* on its hosts have not been scientifically studied, but Roberts (1936) mentioned that in Queensland, three puppies were killed by severe infestations of *H. spiniger* (=*H. longitarsus*). Hoffman (1930) reported that several dogs in Puerto Rico were so heavily infested that rubbing one's hand over the rump dislodged hundreds of lice. Nelson (1962) referred to an emaciated dog in Kenya as "heavily infested." Kittens in rather poor physical condition were infested with *H. spiniger*, which had presumably transferred from dogs in an adjacent animal house. The infestation was well established, as about 50 lice of both sexes and various stages of growth were collected from the kittens (Colless 1959).

In Egypt, Amin and Madbouly (1973) examined 685 domestic dogs and found that only 5% were infested with *H. spiniger* and that the average number per infested dog was fewer than 6 lice. They also noted that all infested dogs were from the warmer and more arid southern Nile Valley and that more lice were found in May than in November–December. The male-female ratio of the lice was approximately 2:1 in their study. On Okinawa, Ryukyu Islands, Pennington and Phelps (1969) found that 22 of 31 dogs examined by them were infested with *H. spiniger*. They collected an average of 47 lice from each infested dog; the maximum number recorded from a single dog was 323. Nelson (1962) noted that almost all the *H. spiniger* that he had collected from dogs had blood in the midgut.

Heterodoxus spiniger is one of several ectoparasites of dogs that serve as an intermediate host of helminthic endoparasites of canines. It has been found to harbor developmental forms of a tapeworm, *Dipylidium caninum*, and a filarial worm, *Dipetalonema reconditum*. The cestode, *D. caninum*, is an intestinal parasite of dogs, foxes, cats, and occasionally humans (Kettle 1984). Yutuc (1975) found a low incidence of tapeworm cysticercoids in specimens of *H. spiniger* (=*H. longitarsus*) collected from dogs in the greater Manila area, Philippine Islands. He referred to the tapeworm as *Dipylidium sexcoronatum*, but it was probably *D. caninum*. After eggs of the tapeworm have been ingested by the louse and have hatched, the cysticercoids develop in the hemocoel of the louse, an intermediate host that also serves as a vector. The life cycle is completed when a dog swallows an infected louse and the contained cysticercoid develops into an adult tapeworm (Voge 1973).

Heterodoxus spiniger has also been reported as an intermediate host of a nematode parasite, *Dipetalonema reconditum* (Nelson 1962). The adult nematodes localize in subcutaneous tissues of dogs, jackals, and hyenas and produce large numbers of microfilariae, which live in the circulating blood. The intermediate host becomes infected by feeding on blood, and the microfilariae pass through the louse's gut wall and move to the fat bodies. Three larval stages are found in the intermediate host, and the life cycle is completed after the louse is swallowed by a dog. In contrast to the dog heartworm, *Dirofilaria immitis, D. reconditum* apparently does not seriously injure dogs. Pennington and Phelps (1969) found that 23% of dogs surveyed on Okinawa, Ryukyu Islands, were infected with *D. reconditum* and that most dogs were infested with *H. spiniger* and with the flea, *Ctenocephalides canis*. Larvae of *D. reconditum* were recovered from both ectoparasites. Although the infection rate of fleas (70%) was much higher than that of lice (40%), the dogs were infested with about four times more lice than fleas.

FAMILY GYROPIDAE

Ewing (1924) characterized Gyropidae as having the following: a single claw on each leg of the two posterior pair; some legs modified into hair-clasping organs (except in one genus); the maxillary palpus two-, three-, or four-segmented; antennae four-segmented but often appearing to have only three segments; and the head having broad, deep antennal fossae and a rounded temporal region. Ewing divided the family into three subfamilies: Protogyropinae, Gyropinae, and Gliricolinae. Clay (1970) agreed that the family consisted of three groups that resemble each other in the characteristics of the mouthparts, general chaetotaxy of the head and abdomen, presence of antennae and antennal sensilla, reduction of sclerotization of the tentorium, and presence of spiracles and the postspiracular setal complex on the lateral plates. However, morphologically, members of the family may vary considerably. In the genus *Macrogyropus*, leg 1 may have two tarsal claws, and legs 2 and 3 may be single-clawed; all legs in the genus *Protogyropus* have a single unmodified claw; and in the genera *Gyropus* and *Gliricola*, one pair of legs may be highly modified for clasping hairs.

Emerson and Price (1975) described six new species of Gyropidae. In their host-parasite list, Emerson and Price (1981) placed 8 genera and 65 species (5 of the species contain 14 subspecies) in the family. Cicchino and Castro (1990) described *Gyropus persetosus* from a spiny rat, *Proechimys albispinus*. The one specimen of *Gliricola palladius* collected by Linardi et al. (1991) from *Oxymycterus rutilans* (Rodentia: Cricetidae) in Brazil may have been a straggler. Price and Timm (1993) described two new species of *Gliricola* from the spiny tree rat, *Mesomys hispidus*, in Peru.

Except for two species, all Gyropidae are parasites of cavies (guinea pigs and their close relatives, Rodentia: Caviidae) and spiny rats (Rodentia: Echimyidae) and their relatives in six other rodent families. One of the exceptions is *Aotiella aotophilus*, a parasite of a night monkey in South America. The second exception is *Macrogyropus dicotylis* from two species of peccaries in Central and South America. Whitaker and Abrell (1987) noted that a collared peccary in Paraguay was infested with 60 *M. dicotylis*. Emerson (1972c) included *M. dicotylis* from the collared peccary in his list of mammalian lice of North America.

The geographical range of the Gyropidae, like that of their wild hosts, is limited to the Neotropical Zoogeographical Region. However, the oval guinea pig louse, *Gyropus ovalis* (figs. 10, 11), and the slender guinea pig louse, *Gliricola porcelli* (fig. 12), accompanied domesticated guinea pigs when they were carried to other continents, and distribution of the lice is now cosmopolitan. The nutria or coypu (*Myocastor coypus*, Rodentia: Capromyidae) was also introduced to North America from southern South America, but many of these rodents now live in the wild in North America, especially in the southeastern United States. Kim et al. (1990) reported the occurrence of a gyropid louse, *Pitrufquenia corpus*, on nutria in North America.

No published reports of the life cycle of a gyropid have been found, but fragmentary biological studies of the slender guinea pig louse and the oval guinea pig louse have been reported. Ewing (1924) observed that both species cling to hairs and remain close to the host's skin. Nymphs and adults are found together in the same location (Kim et at. 1973). Also, the eggs are near the skin; usually only one egg is attached to a hair, near the base of the hair.

Ewing (1924) also saw females and males coupled together and males with extruded spermatophores (Ewing's "ejaculatory sacs"). Deoras and Patel (1960) found that males outnumbered females in the body areas with the most lice but that females outnumbered males in other body areas.

Ewing observed that the oval guinea pig louse readily moves sideways from hair to hair but that the slender guinea pig louse is more likely to go forward or backward on one hair, not sideways. The oval guinea pig louse concentrates on the host's head, but the slender guinea pig louse can be found on all parts of the body, including the head. However, it is found in greatest numbers on the midbody (Deoras and Patel 1960).

Infestations of both lice are usually light, and lice may not be noticed during routine handling of guinea pigs. But large numbers are occasionally seen, and they are usually the slender guinea pig louse. Hopkins (1949) cited Werneck (1942), who mentioned that guinea pigs may be infested with 2,000–3,000 slender guinea pig lice. Caretakers sometimes see large numbers of lice crawling about on the outside of the hair of dead guinea pigs that have lost their body heat.

Both species of guinea pig lice apparently feed on skin debris in much the same way as do other chewing lice. From his studies of lice on a host, Ewing (1924) decided that the lice do not feed on hair or even on minute particles of hair and that it is more likely that they feed on secretions from oil (sebaceous) glands that accumulate in the hair follicle. It is generally agreed by all writers that guinea pigs are seldom seriously injured by lice but that heavy infestations may cause hair loss and a rough hair coat. Lice may be only an indirect cause of these injuries; the direct cause may be excessive scratching by lousy guinea pigs (Owen 1968).

FAMILY LAEMOBOTHRIIDAE

When the family Laemobothriidae was established by Mjöberg (1910), all species were placed in *Laemobothrion* (figs. 13–16), a genus named by Nitzsch (1818). This classification remained unchanged until Ewing (1929) divided the genus by leaving the species from birds of prey in *Laemobothrion* and moving the species from all other birds to his new genus, *Eulaemobothrion*. More recent workers recognized the two groupings as valid but reduced Ewing's *Eulaemobothrion* to subgeneric rank (Hopkins and Clay 1952, Nelson and Price 1965, Emerson 1972b). Of the eight species of Laemobothriidae listed by Emerson from North America north of Mexico, half were in each of the

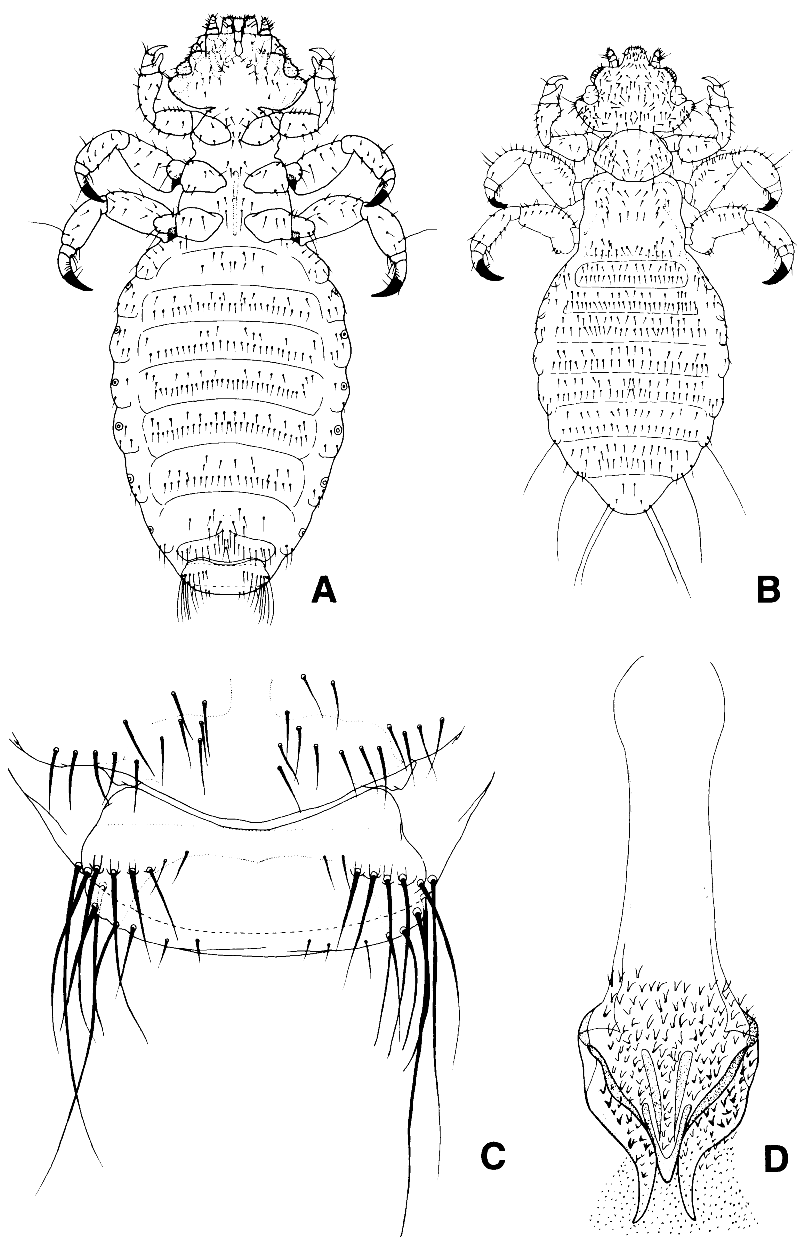


Figure 10. *Gyropus ovalis* (oval guinea pig louse): ***A***, Ventral view of female; ***B***, dorsal view of male; ***C***, female terminalia; ***D***, male genitalia. Redrawn with minor modification by Wen Sam Wang from Emerson and Price (1975); courtesy of Brigham Young University Science Bulletin, Biological Series.

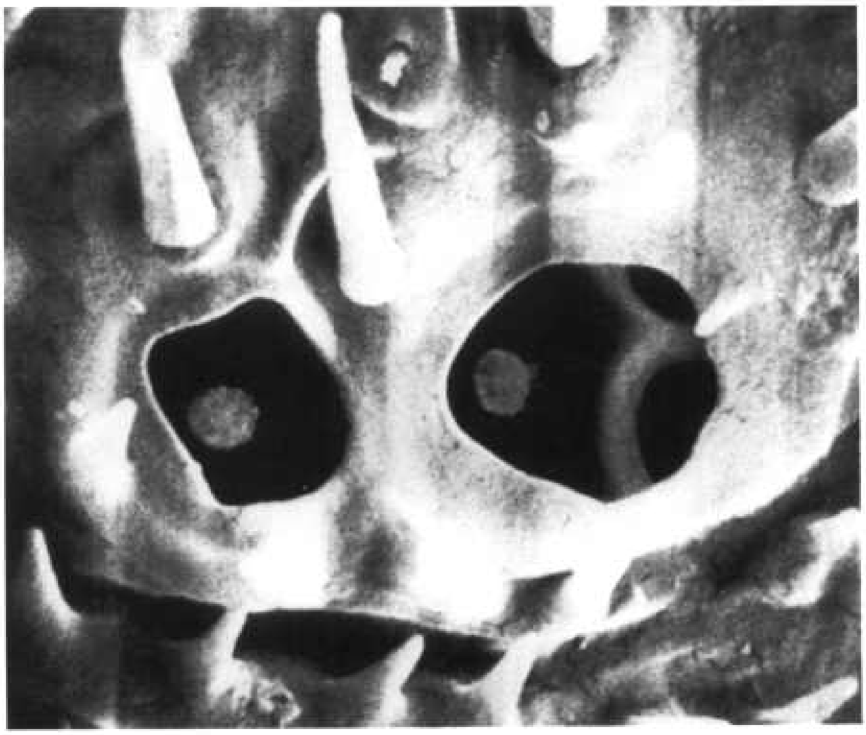


Figure 11. *Gyropus ovalis*: Antennal sense organ. SEM × 3,870. From Clay (1970), reprinted by permission of publisher. © British Museum (Natural History), 1970.

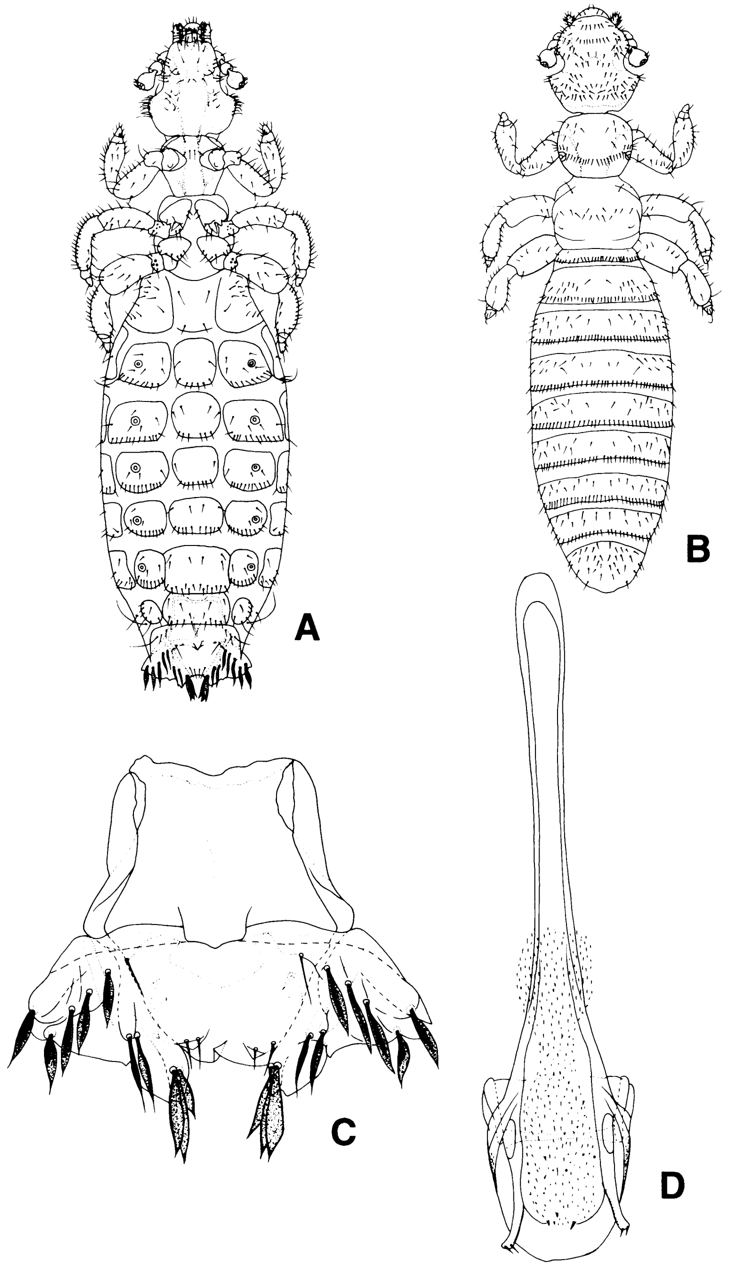


Figure 12. *Gliricola porcelli* (slender guinea pig louse): ***A***, Ventral view of female; ***B***, dorsal view of male; ***C***, female terminalia; ***D***, male genitalia. Redrawn with minor modification by Wen Sam Wang from Emerson and Price (1975); courtesy of Brigham University Science Bulletin, Biological Series.

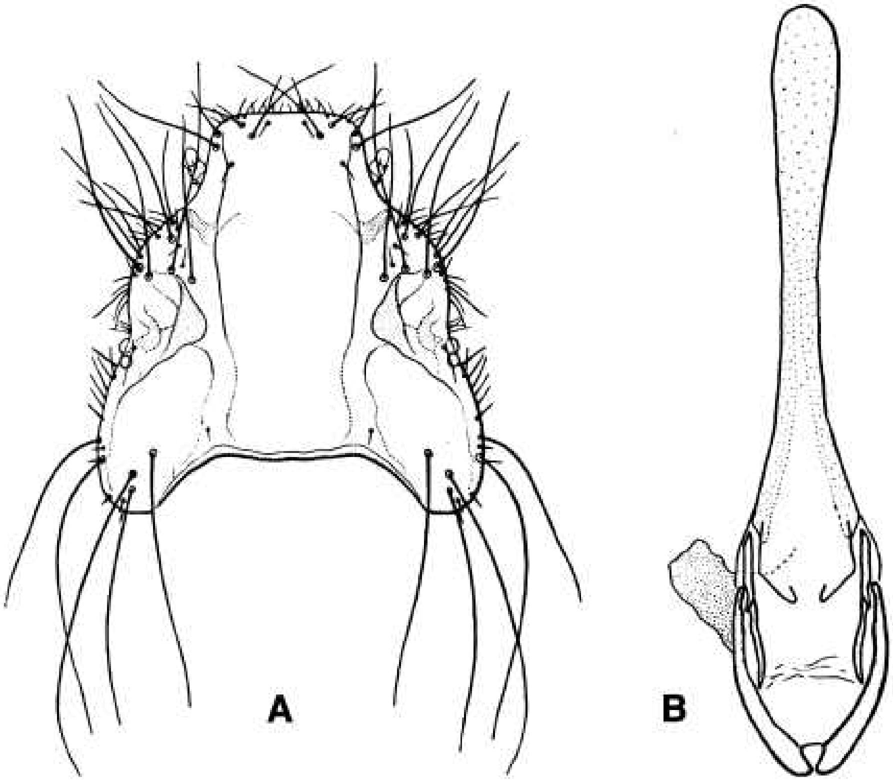


Figure 13. Male *Laemobothrion tinnunculi*: ***A***, Dorsal view of head; ***B***, genitalia. From Clay and Hopkins (1950), reprinted by permission of publisher. © British Museum (Natural History), 1950

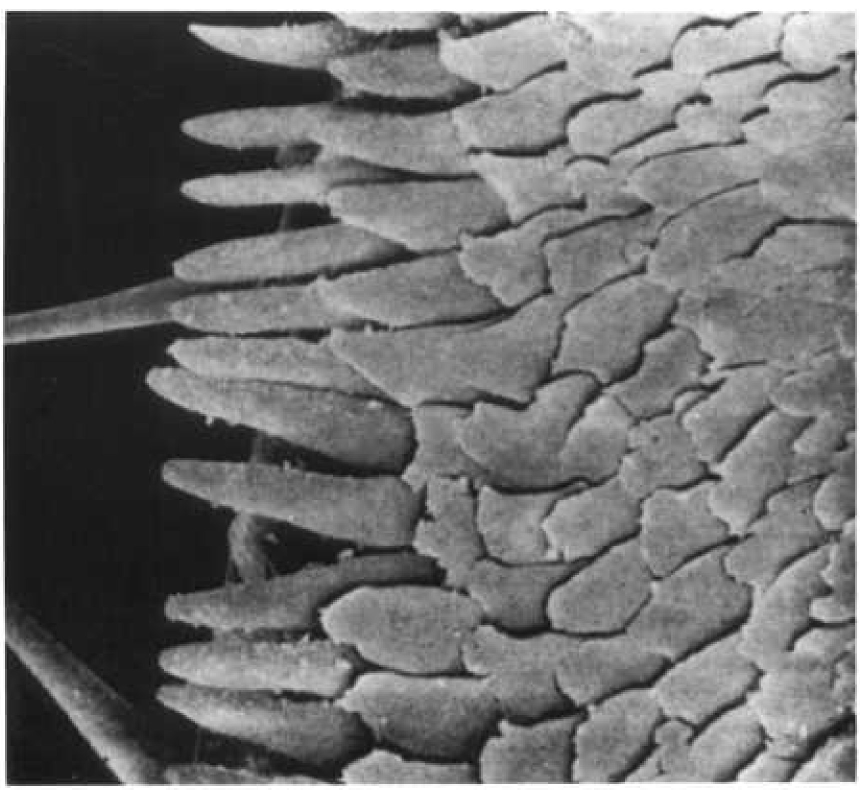


Figure 14. *Laemobothrion chloropidis*: Edge of temple. SEM × 886. From Clay (1970), reprinted by permission of publisher. © British Museum (Natural History), 1970.

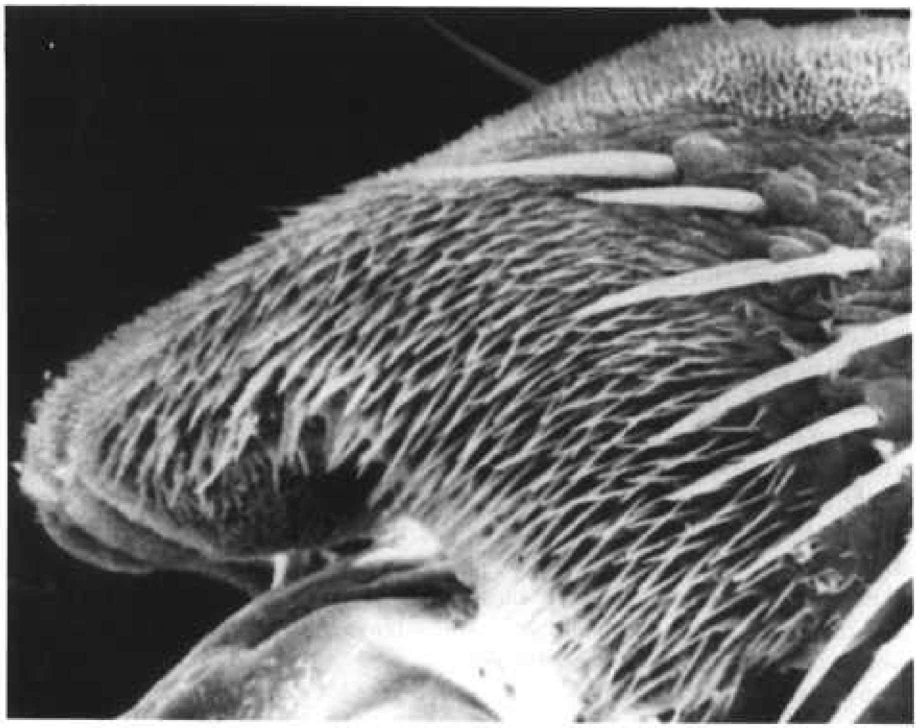


Figure 15. *Laemobothrion vulturis*: Distal end of tibia. SEM × 400. From Clay (1970), reprinted by permission of publisher.

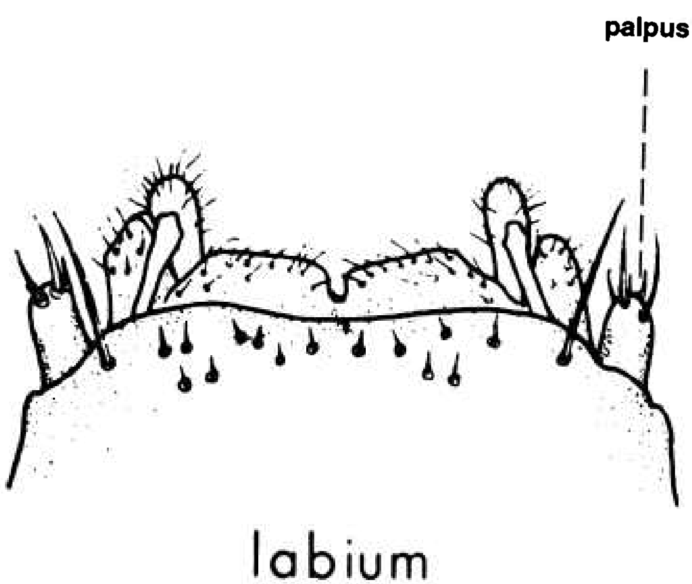


Figure 16. Labium of *Laemobothrion* sp. Note presence of palpi. From Calaby (1970), reprinted by permission of Melbourne University Press.

two subgenera. An additional three valid species of *Eulaemobothrion* from other regions were listed by Clay and Hopkins (1960).

The Laemobothriidae are large lice; for example, the average length of a group of female *Laemobothrion vulturis* was 10.61 mm (Nelson and Price 1965).

The family is distinguished from other Amblycera by having a sculptured area on the temples (posterolateral margins of the head) with outer rows of peglike projections (figs. 13,14), femur III with a ventral area of microtrichia, and distal ends of tibia II and III with terminal dorsal patches of microtrichia (fig. 10C) (Nelson and Price 1965, Clay 1970). Figure 16 shows details of the labium of *Laemobothrion* sp., and figure 17 is a scanning electron micrograph of the combs on the abdominal sternites of *Laemobothrion vulturis*, a parasite of the bald eagle, golden eagle, and other birds of prey (Emerson 1972b). *Laemobothrion maximum* (and three other species of chewing lice) were collected from a vulture (*Buteo buteo*) in Spain by Perez-Jimenez et al. (1994).

Apparently the Laemobothriidae do not parasitize domestic fowl. Species of the subgenus *Laemobothrion* have been collected from many birds in the order Falconiformes: the California condor, turkey vulture, black vulture, many species of hawks, the osprey, crested caracara, peregrine falcon, sparrow hawk, golden eagle, bald eagle, and two sea eagles. The subgenus *Eulaemobothrion* parasitizes water birds in the order Ciconiiformes (storks and ibises) and the order Gruiformes (rails, coots, gallinules, limpkins, and grebes).

FAMILY MENOPONIDAE

Menoponidae is the largest of the families of Amblycera. It occurs worldwide and all of the species are ectoparasites of birds. Clay (1969) provided a key to the 47 genera recognized by her. Although the validity of many genera is doubtful, Butler (1985) mentioned that over 50 genera are known; it is believed that there may be as many as 60. Emerson (1972b) listed 35 genera from North America north of Mexico.

Many genera of Menoponidae are considered host specific because they seem to be restricted to a single group of birds: a single family or a single order. But other genera parasitize a much wider variety of birds. For example, there are records of *Menacanthus* complex from five orders of birds and *Colpocephalum* complex from seven orders of birds (Clay 1957). The *Menacanthus eurysternus* complex is known from 20 families (70 genera and 118 species) of passerine birds as well as from the order Piciformes and perhaps 3 other orders (Price 1975).

Menoponid lice have a broadly triangular head that is expanded behind the eyes (fig. 18). The maxillary palpus is four-segmented; the labial palpus is present, usually one-segmented, and has five distal setae. The antennae may be four- or five-segmented. If four-segmented, it has two adjacent sensilla on the terminal segment; if five-segmented, it has one sensillum on each of segments 4 and 5. The thoracic segments are not fused and are separate from tergum 1. The mesonotum does not have seta-bearing protuberances. Legs 2 and 3 have two tarsal claws. The family is separated from Boopiidae in that the spinelike processes on the underside of the head (see fig. 6) are reduced or absent and the antennae are not strongly clubbed.

Species of Menoponidae are found on a wide variety of birds: albatrosses, pelicans, cormorants, tinamou, magnificent frigate bird, herons, spoonbills, ducks, geese, swans, vultures, eagles, hawks, chickens, turkeys, cranes, snipes, curlews, gulls, pigeons, parrots, owls, cuckoos, bee-eaters, woodpeckers, sparrows, and passerine songbirds. Clay (1957) stated that 19 orders of birds harbor menoponids, and Calaby (1970) remarked that they "occur on all birds that have been sufficiently studied."

Most Menoponidae are active lice that move about on the body of their hosts, but some of the genera have unusual habitats. Species of *Actornithophilus*, *Comatomenopon*, and *Somaphantus* live inside the quills of the primary and secondary feathers of their hosts (Emerson 1958; Clay 1962; Tuff 1967), and apparently all stages of development are found in that microhabitat. The eight known species of *Piagetiella* live inside the pouch of pelicans and a few species of cormorants, where they firmly attach themselves by clasping the lining with their mandibles (Price 1970, Askew 1971). They leave the pouch only to oviposit on the feathers. Other menoponids from pelicans and cormorants are in the genera *Austromenopon* and *Eidmaniella* (Green and Palma 1991, Martin-Mateo 1992b).

Because of the popularity and high monetary value of poultry, the menoponids of chickens and waterfowl have received more study than other genera. Emerson (1972d) listed 18 species of Menoponidae in 7 genera known from gallinaceous birds of North America. But *Menacanthus* and *Menopon*, along with *Trinoton* from ducks and geese, are the genera that concern poultry owners. *Amyrsidea megalosoma* was said by Payne et al. (1990) to be a widely distributed parasite of ring-necked pheasants in Nebraska.

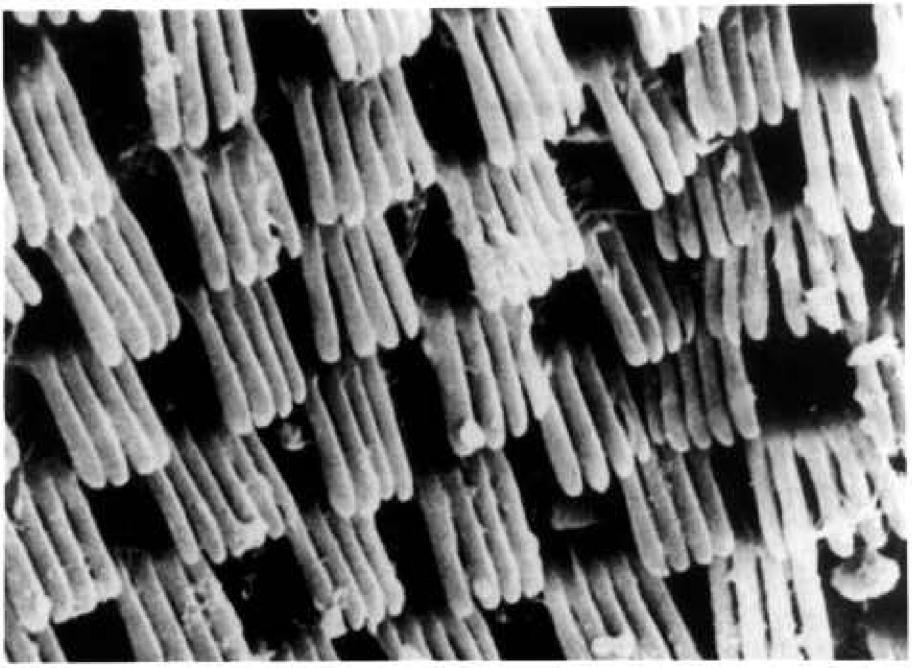


Figure 17. *Laemobothrion vulturis*: Combs from abdominal sternite. SEM × 867. From Clay (1970), reprinted by permission of publisher. © British Museum (Natural History), 1970.

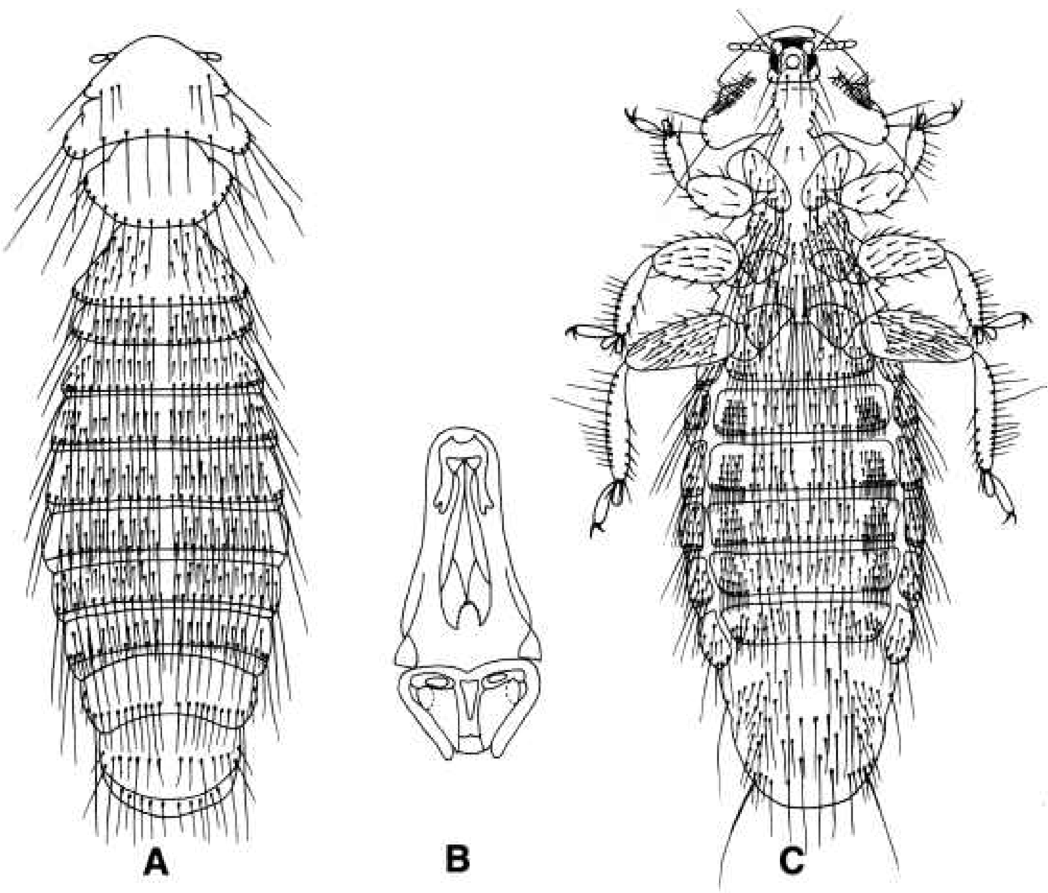


Figure 18. Male *Menacanthus stramineus* (chicken body louse): ***A***, Dorsal view; ***B***, genitalia; ***C***, ventral view. Redrawn with minor modification by Wen Sam Wang from Emerson (1956); courtesy of Journal of Kansas Entomological Society.

Genus *Menacanthus*

The large, economically important genus *Menacanthus* has a worldwide distribution and a wide range of avian hosts. At one time, more than 130 species were listed as parasites of birds in 3 orders: Galliformes, Piciformes, and Passeriformes (Wiseman 1968). However, as indicated by Emerson's (1972d) comment that "an adequate study of the genus is not available," many of the original names of those species were of doubtful validity. Price and Emerson (1975) placed 19 of the previously recognized 26 species and subspecies from woodpeckers and related birds (Piciformes) in synonymy, and Price (1977) reduced the number of species from passerine birds from 94 to 28. A similar reduction in the number of valid species from chickens, guinea fowl, peafowl, and bobwhites (Galliformes) can be anticipated. Emerson (1972b) listed 41 species of *Menacanthus* known to occur in North America north of Mexico, and Price and Clayton (1994) described 14 species from antbirds, ovenbirds, and tapaculos. Martin-Mateo (1989) listed 15 species of *Menacanthus* from Spain, but 6 are treated as synonyms of *Menacanthus eurysternus* (broad sense) by Price (1977).

Menacanthus can be separated from *Menopon*, which also parasitizes chickens, by the presence of two short, spinelike processes on the underside of the head (see fig. 6) (Tuff 1977). The terminal segment of the antenna is not divided and has numerous ridges close together (fig. 19). The egg of *Menacanthus* sp. has a distinctive operculum that is elaborately sculptured and that has 4–8 plumelike processes attached to the tip of the operculum (fig. 20) (Foster 1969).

Menacanthus stramineus (chicken body louse)

The best known species of this genus, *Menacanthus stramineus,* (fig. 18) is a pale-yellow louse about 3–4 mm long that has numerous short setae on the dorsal surfaces of the mesothorax and metathorax. Each abdominal segment has two rows of posteriorly directed setae on its dorsal surface (Fairchild and Dahm 1954). The chicken body louse is a cosmopolitan species that is found on poultry worldwide. It can be separated from another *Menacanthus* of chickens, *M. cornutus,* by the presence of more metathoracic setae (fig. 21). Lonc et al. (1992) reported morphometric differences between Polish and Indian collections of the chicken body louse; among other characteristics, Polish lice were larger and less variable. From a biometrical analysis of nine measurements of poultry lice, Lonc (1990a) concluded that measurements of head length and body length were the most useful for statistical study.

Life history. The intricately frilled egg (fig. 22) of the chicken body louse is most frequently placed on the lower barbs of the host's feathers. If the chicken is heavily infested, large clusters of eggs may be seen on the sparse feathers below and around the vent and may also be found on the small feathers on the lower head and throat, and under the wing.

The eggs of *M. stramineus* hatch 4–7 days after they are deposited. At a constant 35 °C and 95% relative humidity, they hatch in 4–5 days (Stockdale and Raun 1965). In general, nymphs are found on the host's skin mingled with adult lice and in the same body areas. But Brown (1970) noted that while nymphs outnumbered adults under the wing, adults were more numerous in other body areas. Under optimum conditions, nymphal growth and metamorphosis proceed rapidly; a nymphal molt occurs each 3 days, and the molt from nymph to adult occurs 9 days after eggs hatch. However, 11–16 days are sometimes required for nymphal development.

Apparently adult *M. stramineus* are not sexually mature until about the fourth day of adult life, because eggs laid by younger females do not hatch (Stockdale and Raun 1965). Females 5–6 days of age laid more eggs per day, up to a maximum of four, than did younger or older females. The average egg production was 1.6/days or about 20 eggs/female. When males were not present, females oviposited but the eggs did not hatch.

In spite of what appears to be low fecundity, the number of chicken body lice on an individual bird can increase rapidly under optimum conditions. Stockdale and Raun (1960) recorded that 16 wk after a hen had been infested with 3 lice, it had an infestation of more than 12,000 nymphs and adults.

Host-parasite relationships and economic importance. Because *M. stramineus* has never been found on any other wild bird host, it is presumed that the wild turkey was its original host and that the louse transferred to domestic poultry. It is now quite common on both chickens and domestic turkeys (Clay 1957, Emerson 1962c) and is the most common louse on chickens in the United States (DeVaney 1976), including modern poultry production facilities (Axtell and Arends 1990). *Menacanthus stramineus* is also a parasite of domestic guinea fowl, peafowls, quail, and pheasants. Emerson (1956) noted that it is frequently found on those birds if they are hatched under chickens or maintained in zoological gardens. Chicken body lice that become separated from their host probably do not survive more than 24 hr (Furman 1962).

The chicken body louse is occasionally found on domestic ducks and geese, especially on those that mingle with barnyard flocks of chickens and turkeys, but does not seem to maintain self-sustaining populations on them (Price et al. 1969). An apparently rare

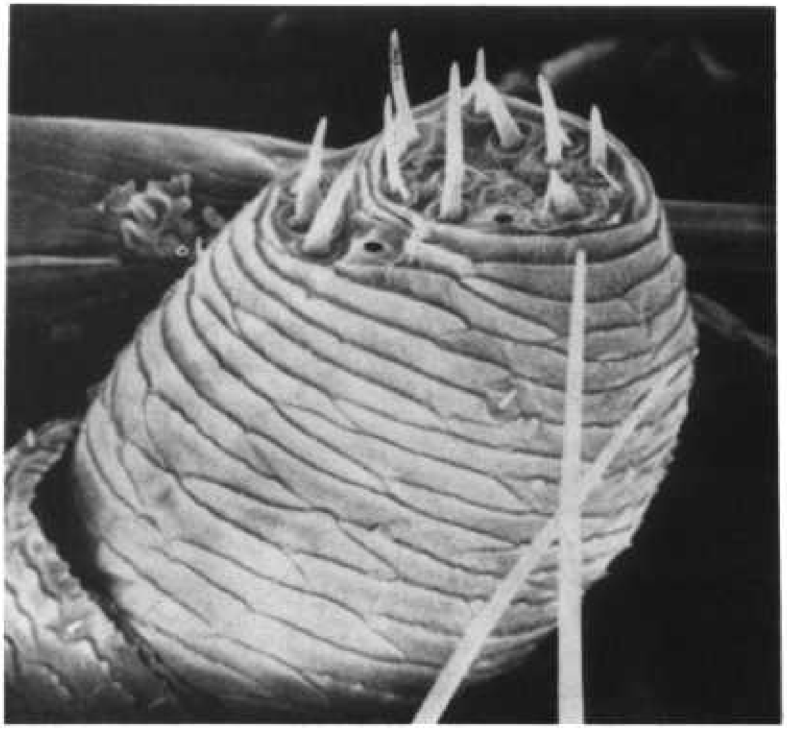


Figure 19. *Menacanthus stramineus*: Terminal segment of antenna. From Clay (1969), reprinted by permission of publisher. © British Museum (Natural History), 1969.

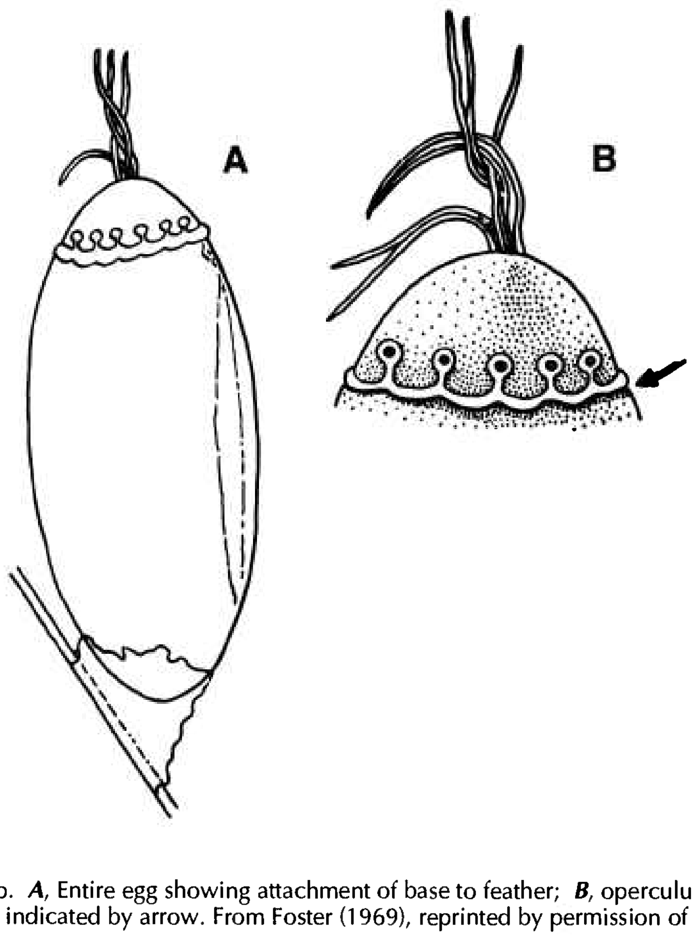


Figure 20. Egg of *Menacanthus* sp. ***A***, Entire egg showing attachment of base to feather; ***B***, operculum with its plumes and sculpturing, and its line of fissure indicated by arrow. From Foster (1969), reprinted by permission of Journal of Parasitology.

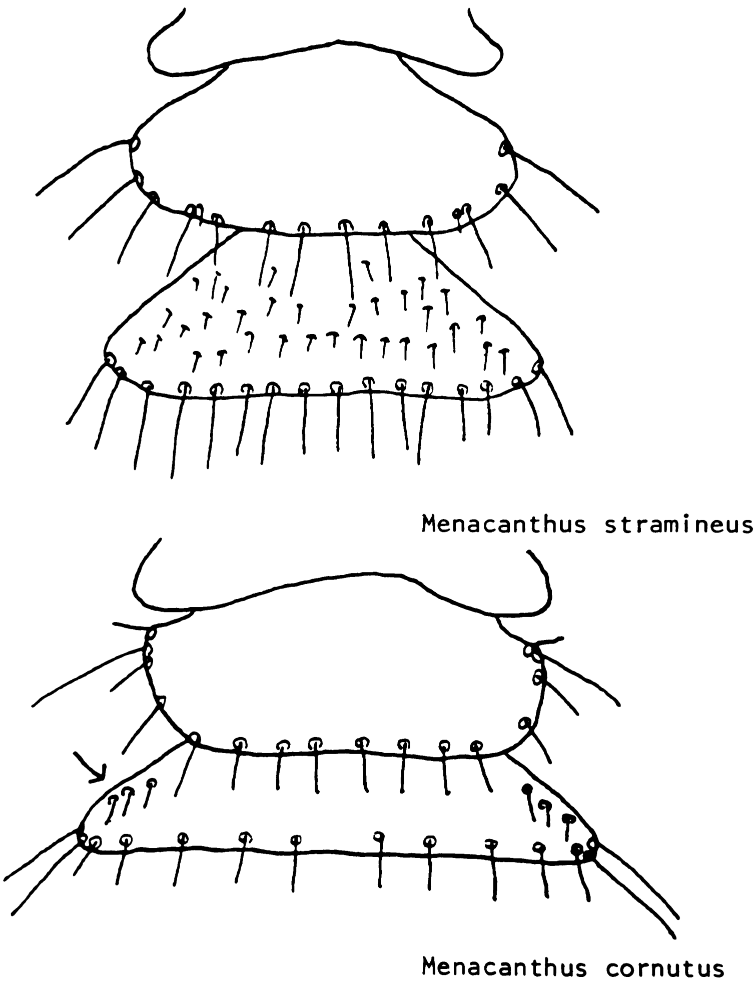


Figure 21. Separation of *Menacanthus stramineus* and *M. cornutus*. Only a few short setae (arrow) are present on dorsum of the metathorax of *M. cornutus*, and they are on the lateral margins. From Tuff (1977), reprinted by permission of Texas Journal of Science.

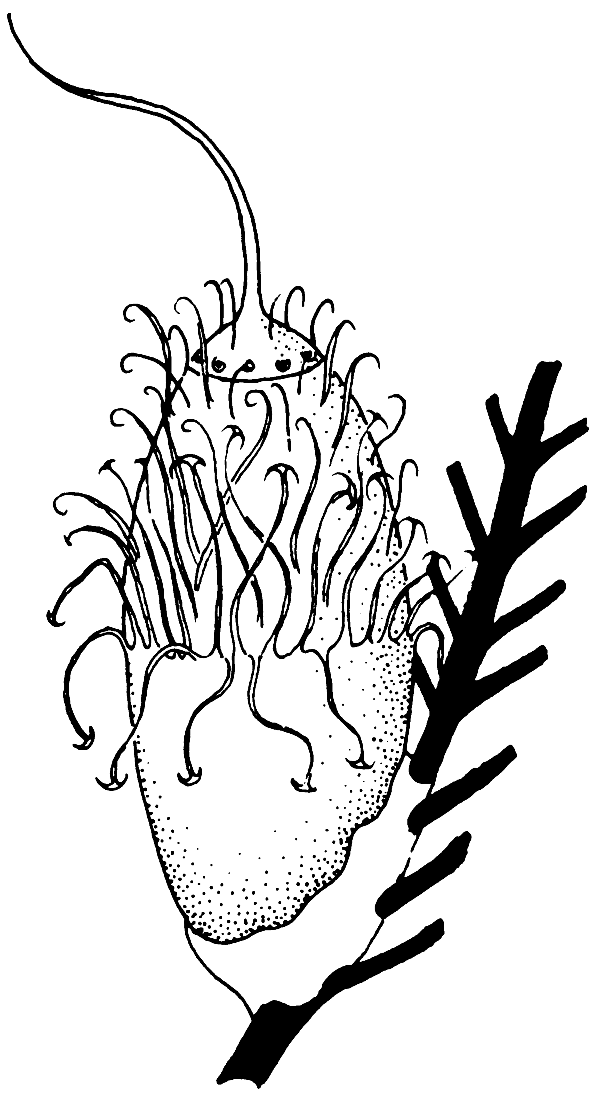


Figure 22. Egg of *Menacanthus stramineus*. From Marshall (1981), reprinted by permission of Academic Press Ltd, London.

infestation of pigeons was reported by Brown (1971). Presumed stragglers of *M. stramineus* were collected from goats and dogs in northern Nigeria by George et al. (1992). Rodents may be involved in the spread of *M. stramineus* from bird to bird (DeVaney et al. 1980, Axtell and Arends 1990).

In contrast to other species of chicken lice, the chicken body louse is usually found on the host's skin rather than on the feathers. Many writers have noted that *M. stramineus* is most easily found by parting the feathers on the rear of the bird, because the lice tend to congregate around and below the vent where the feathers are short and sparse. Trivedi et al. (1990) noted that *M. stramineus* sometimes invades body orifices such as the cloaca. However, this louse also inhabits other body areas and is sometimes seen on the lower head, neck, and legs and under the wings. In a survey of chickens carried out in Dehradun, India, Trivedi et al. (1991) recovered 44% of chicken body lice from the abdomen, 18% from the breast, and 20% from the back.

In fact, lice can be found on any part of the body of a heavily infested chicken (Bishopp and Wood 1917b, DeVaney 1976). A correlation between lower host skin temperatures and louse numbers was found by Brown (1970), who noted that skin temperature in the anal region of hens was about 4 °C lower than temperature under the wing and almost 6 °C lower than the rectal temperature. Louse counts made at the same time revealed that the anal region was heavily infested with adult lice but had only a few nymphs, whereas only a few adults and many nymphs were found under the wings.

Brown (1970) noted, however, that the distribution of lice on the chicken's body may also be influenced by relative humidity and by the chicken's preening activity. Brown (1974) observed that White Rock roosters infested with more than 11,000 *M. stramineus* per bird groomed themselves 11 times more frequently than those that had a median infestation of 292 lice.

Although the chicken body louse usually remains on the host's skin, Crutchfield and Hixson (1943) examined lice soon after removal from the host and found bits of feather barbs and barbules and some foreign debris in the crops of the lice but no epidermal scales. In addition, most of the crops contained nucleated red blood cells, and blood pigment was found in the gut. Wilson (1933) had earlier suggested that *M. stramineus* habitually includes host blood in its diet and frequently obtains blood by chewing the tender quills of new feathers that are pushing through the host's skin. In Crutchfield and Hixson's study, chickens that were heavily infested with chicken body lice had not only more injured quills that were easily induced to bleed but also more skin injury, namely, large skin areas with tiny blood clots, sloughing scabs, and oozing serum. Injured skin areas were also the areas that contained the largest numbers of lice.

By radiolabeling host blood corpuscles, Derylo and Gogacz (1974) measured the quantities of blood consumed by *M. stramineus*. The possible transmission of disease organisms by lice has been investigated; the virus of eastern equine encephalitis (Howitt et al. 1948) and a bacterium (*Pasturella multocida*) that causes fowl cholera (Derylo 1970) have been isolated from the chicken body louse.

Individual birds in a flock of poultry vary greatly in their susceptibility to lice. Although it has often been suggested that malnourished, unthrifty chickens are expected to be more heavily louse infested than are well-tended ones, Kartman (1949) was unable to demonstrate a cause-effect relationship. In his experiments, severely undernourished hens supported fewer lice than did hens that had received a normal ration, but all infestations were low—fewer than 40 lice per bird. In those experiments, louse populations were influenced more by the host's self-grooming activity than by the host's nutrition. Kartman observed that debeaked chickens were more severely infested than were their counterparts with normal beaks. In more elaborate studies, Brown (1972) and DeVaney (1976) confirmed that debeaked birds, whose normal preening activities were greatly hampered, are rapidly infested with large numbers of lice—sometimes as many as 20–50 times the number on normal chickens.

Quigley (1965) decided that susceptibility to the chicken body louse may be influenced by an unknown factor that is inherited from female parents. He showed that certain dam families were infested with significantly larger numbers of chicken body lice than were others of the same breed and background.

Examination of the skin of chickens that are heavily infested with *Menacanthus stramineus* reveals patches of skin with scabs, dried blood, and other injuries. The skin areas where the lice congregate often have a crusty appearance (Bishopp and Wood 1917b). The economic importance of these injuries, of the restlessness of the birds, and of the resulting losses in body weight and egg production vary with severity of the infestation, poultry husbandry practices, and other practical considerations. Matthysse (1972) and Loomis (1978) pointed out that in modern caged layer and broiler operations, chickens are seldom infested with damaging numbers of lice.

In certain experiments, egg production and weight gains did not improve significantly when lice were controlled (Edgar and King 1950, Stockdale and Raun 1960, Tower and Floyd 1961). But in those experiments, hens were often lightly infested in the early part of the egg production cycle and became moderately infested only near the end of the cycle, when egg production is expected to decline. Derylo (1974b) reported that White Leghorn hens lightly infested with *M. stramineus* laid 10% fewer eggs than uninfested hens. In weight-gain studies, infested Rhode Island hens gained 375 g less in 80 days than did uninfested ones, and infested Beltsville turkeys gained 330 g less in 70 days than did uninfested controls (Derylo 1974c). An important decrease in egg production was reported by Gless and Raun (1959); the decrease was more than 50% after infestations exceeded 20,000 lice per bird. DeVaney (1976), who used debeaked hens that were soon heavily infested with chicken body lice (more than 10 lice seen each time the feathers were parted), found that egg production declined by 16% in young hens and 46% in older hens.

In other weight-gain studies, louse-infested chickens also do not gain as much weight as uninfested ones. Derylo and Mart (1969) found that uninfested control chickens gained about 15% more weight in 10 wk than did those infested with *M. stramineus.* DeVaney (1976) observed that a group of young hens that had been extra heavily infested for 6 wk weighed 450 g, or about 30% less than an uninfested group. Young chicks that are heavily louse infested may die (Loomis 1978).

Drummond et al. (1981) estimated that all poultry lice as a group cause a 7% reduction in poultry weight gains and a 10% reduction in egg production in the United States, an annual loss to the poultry industry of $378 million. It is generally accepted that *M. stramineus* is the most injurious poultry louse, because of its higher incidence and greater prevalence in the United States.

Other species of *Menacanthus*

Although rarer than *M. stramineus*, other species of *Menacanthus* are known to parasitize poultry and game birds in the United States (Emerson 1972d, Loomis 1978). *Menacanthus cornutus* (figs. 23, 24) has been collected from domestic chickens in many parts of the world and is probably more widely distributed in the United States than just Oklahoma, Alabama, and Georgia, the only states from which it has been reported (Emerson 1956). Reid and Linkfield (1957) found two flocks of broilers in Georgia to be so heavily infested that the birds had been injured by the lice; however, they found no other infested flocks in their extensive survey of Georgia poultry farms.

Hafez and Madbouly (1966) included *M. cornutus* in their list of lice from chickens in Egypt but indicated that it was rare. *M. cornutus* was reported by Fabiyi (1988) to be the dominant louse on chickens in Nigeria, with about 4% of birds infested with more than 10,000 lice; he did not find *M. stramineus* in that country. Trivedi et al. (1991) found that in India, *M. cornutus* localized on the back and breast of infested chickens, with lesser numbers recovered from the abdomen and other parts of the body. A first report of the occurrence of *M. cornutus* in India was published by Trivedi et al. (1990) along with confirmation that the louse in almost all stages feeds on host blood.

Menacanthus eurysternus complex has been recorded from 118 species of passerine birds and has a worldwide distribution (Price 1975). As many as 460 lice were recovered from a single myna (*Acridotheres tristis*) by Chandra et al. (1990). They related high populations of *M. eurysternus* to the breeding time of the birds and elevated levels of sex hormones.

Emerson (1972d) listed *Menacanthus numidae* as one of 14 species of Mallophaga that had been collected from guinea fowl in North America north of Mexico and did not list any other host for that species.

Menacanthus pallidulus (figs. 25, 26) has a worldwide distribution and was believed by Emerson (1956) to be quite common on chickens throughout the United States. But because it has been frequently misidentified as an immature *M. stramineus*, there are only a few records of it from the United States.

Menacanthus pricei is a parasite of bobwhite quail (*Colinus virginianus*) in all parts of Texas; it has been reported from Oklahoma, Mississippi, and North Carolina and probably also occurs in Maryland, Virginia, Ohio, and other states with bobwhites (Wiseman 1968). Bobwhites occur from Wyoming to Ontario, and from there south to Florida and west to New Mexico; they are also in Mexico to Chiapas and in Cuba (Sibley and Monroe 1990). Most collectors have commented that *M. pricei* is usually the least numerous of the four species of lice found on bobwhites.

Genus *Menopon*

After Nitzsch (1818) erected *Menopon*, at least 325 species were placed in the genus, but Harrison (1916) listed 133 species that were either synonyms or had been transferred to other genera. Hopkins and Clay (1952) further narrowed *Menopon*. In his review of the genus, Emerson (1954) listed only 10 valid species, and 6 of those were newly described by him. At one time, all *Menopon* (as restricted by Emerson) were parasites of Old World gallinaceous birds, but two species were apparently carried to the New World, where they now occur on many native gallinaceous birds and on domestic poultry (Emerson 1972d).

The *Menopon* are small—usually about 1.5–2.5 mm long. They do not have spinelike processes on the

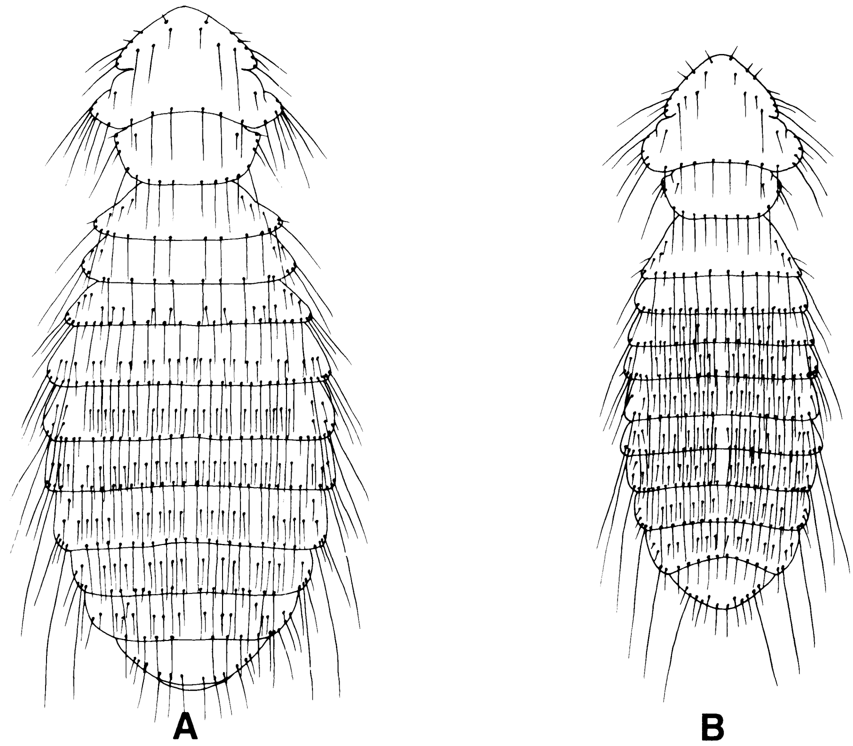


Figure 23. *Menacanthus cornutus*: ***A***, Dorsal view of female; ***B***, dorsal view of male. Redrawn with minor modification by Wen Sam Wang from Emerson (1956); courtesy of Journal of Kansas Entomological Society.

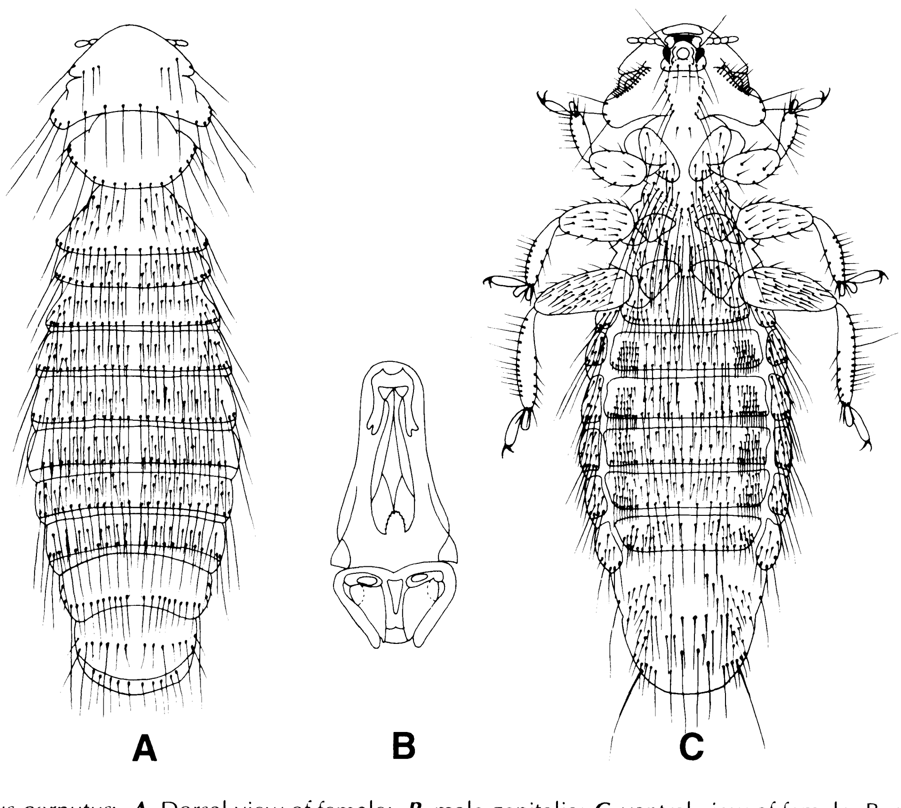


Figure 24. *Menacanthus cornutus*: ***A***, Dorsal view of female; ***B***, male genitalia; ***C***, ventral view of female. Redrawn with minor modification by Wen Sam Wang from Emerson (1956); courtesy of Journal of Kansas Entomological Society.

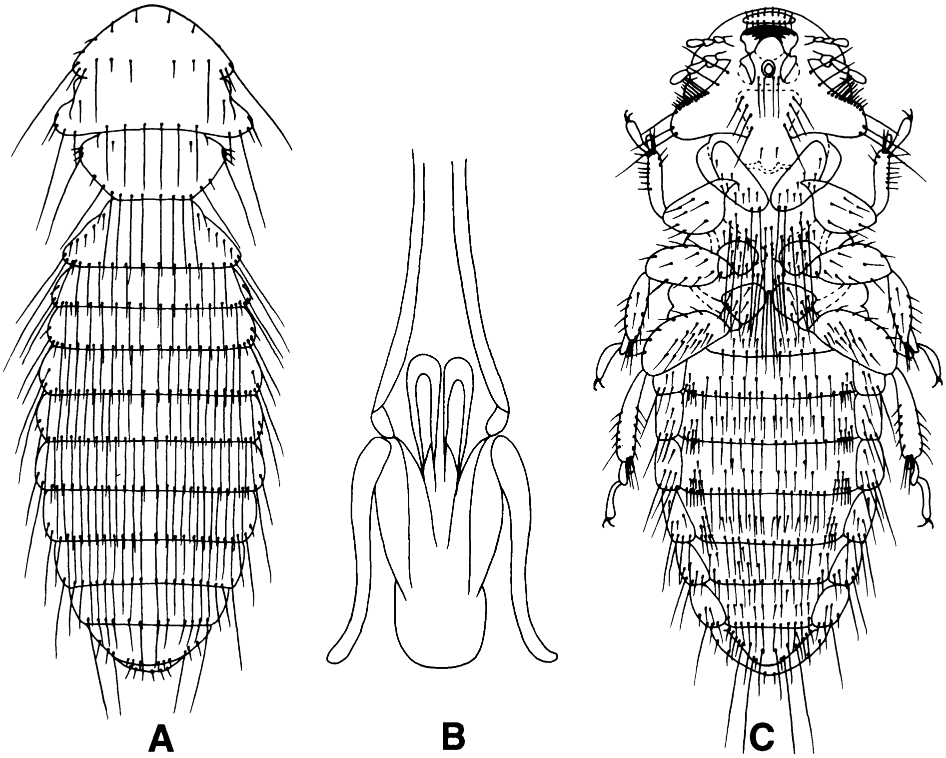


Figure 25. Male *Menacanthus pallidulus*: ***A***, Dorsal view; ***B***, genitalia; ***C***, ventral view. Redrawn with minor modification by Wen Sam Wang from Emerson (1956); courtesy of Journal of Kansas Entomological Society.

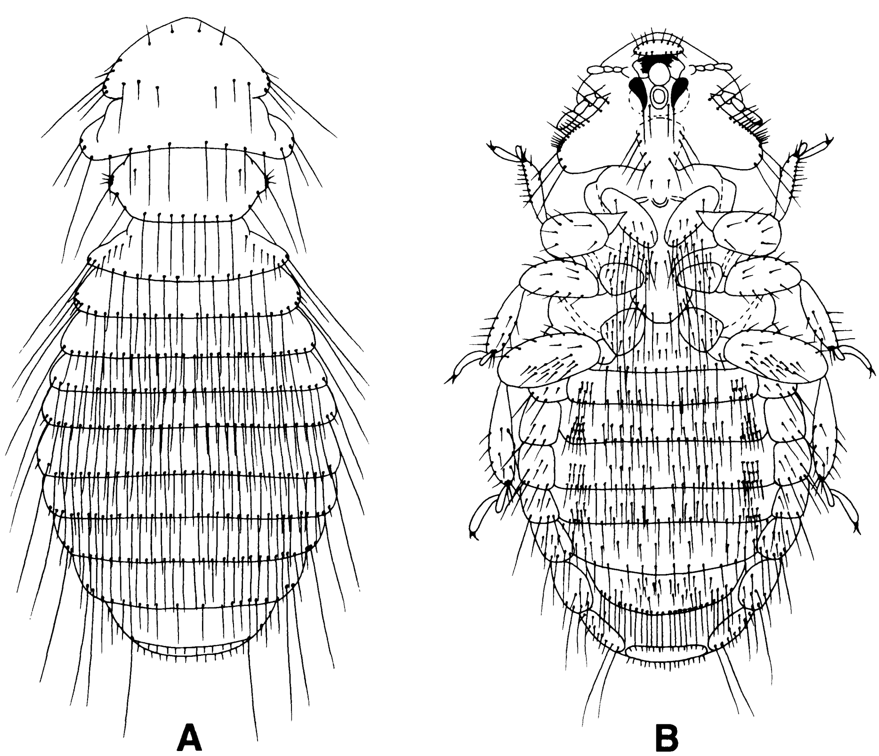


Figure 26. Female *Menacanthus pallidulus*: ***A***, Dorsal view; ***B***, ventral view. Redrawn with minor modification by Wen Sam Wang from Emerson (1956); courtesy of Journal of Kansas Entomological Society.

underside of the head, and they have only one row of setae along the dorsal margins of the abdominal segments.

Menopon gallinae (shaft louse)

As their common name suggests, *Menopon gallinae* (figs. 27, 28) are frequently seen in single file along the shaft of a feather. If the feathers on the thigh and breast of a heavily infested bird are parted, the lice can be seen running down the shaft and dispersing on the skin (Roberts and Smith 1956). But this species does not habitually rest on the skin, as does the chicken body louse. Trivedi et al. (1991) found the shaft louse approximately equally distributed over the back, breast, and abdomen of heavily infested chickens.

The shaft louse is pale yellow and about 2 mm long (Emerson 1956). The eggs are deposited singly at the base of the shaft, but sometimes several eggs are seen close to each other. The life history is not known but is believed to be similar to that of *Menacanthus stramineus*. Bishopp and Wood (1917b) suggested that the shaft louse spends more time in the egg and nymphal stages than do other chicken lice.

In North America the principal host of the shaft louse is the domestic chicken, but guinea fowl are often infested (Price et al. 1969). Pigeons were listed as hosts in Mexico (Hoffmann 1961) and in Cuba (Boado et al. 1992). Turkeys, pheasants, and ducks are also hosts, especially if raised with chickens. Because *M. gallinae* occurs on all but one species of wild chicken in Southeast Asia, it appears that they were the original hosts (Emerson 1956, Emerson and Elbel 1957b).

Studies by Crutchfield and Hixson (1943) indicated that *M. gallinae* feed only on feather particles, but Derylo (1974a) reported that about 2%–7% of the shaft lice examined by him had fed on blood. Joyce A. DeVaney (personal communication) of the Agricultural Research Service's Veterinary Toxicology and Entomology Research Laboratory in College Station, Texas, also observed red blood cells in the digestive tract of a small percentage of shaft lice that she studied. It is believed that the shaft louse is less injurious than the chicken body louse, but Derylo (1974b,c) found that egg production of infested chickens was 9.3% lower than that of uninfested chickens and that body weight was reduced. Okaeme (1989) claimed that severe infestations of chicken lice (all species) caused limb weakness and lameness in as many as 16% of chickens in southern Nigeria.

Menopon pallens

In North America, the chukar (*Alectoris graeca*) and the gray partridge (*Perdix perdix*) are parasitized by *M. pallens* (Emerson 1972b). In other parts of the world, this louse occurs on many species of *Alectoris* and *Perdix*.

Genus *Trinoton*

Hopkins and Clay (1952) recognized 17 valid species of *Trinoton*. The known hosts of *Trinoton* are flamingoes (order Ciconiiformes) and waterfowl in the order Anseriformes. Clay and Hopkins (1960) divided the genus into four species groups: the *femoratum* group on flamingoes, *aculeatum* group on tree ducks (genus *Dendrocygna*), *gambense* group on the spur-winged goose (*Plectropterus gambense*) of tropical Africa, and *querquedulae* group on ducks and geese.

Emerson (1972b) listed four species of *Trinoton* that were known from North America north of Mexico. The two most important are *T. anserinum* from wild and domestic geese and from swans, and *T. querquedulae* from ducks, teals, widgeons, and their relatives. Both species of lice are rather large: 5–6 mm long. Their life history is unknown.

Sarconema eurycerca, a filarial heartworm that inhabits the myocardium of swans, has been shown by Seegar et al. (1976) to use *Trinoton anserinum* as a cyclodevelopmental vector. In their study, 66% of lice had blood in the digestive tract and 60% of lice collected from filaria-infected whistling swans (*Cygnus colombianus*) harbored microfilariae. Frequently, more than one developmental stage of microfilaria was found in the same louse. The late "sausage" stage and the second stage were always found in the abdomen; the larger third stage was most often found in the head but occasionally in the thorax. The large larvae, which leave the vector for a new avian host, were active; they moved back and forth between the head and thorax of the louse, and a few were seen on the external mouthparts. Cohen et al. (1991) confirmed the observations of Seegar et al. but used the mute swan *(Cygnus olor)* as a host for *T. anserinum*.

Genus *Colpocephalum*

Colpocephalum is a large genus with a broad host range. *Colpocephalum turbinatum* is one of four species of Mallophaga that parasitize the domestic pigeon; Nelson (1971) reported colonization of the louse. At 32–37 °C, a generation was completed in 20–30 days.

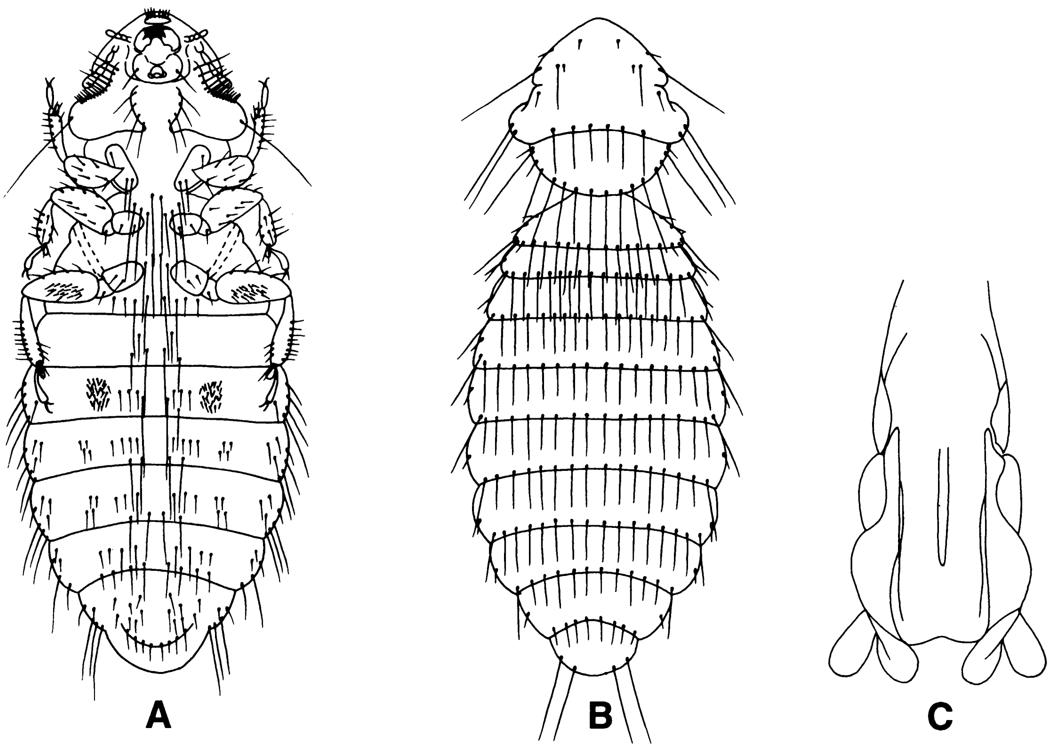


Figure 27. Male *Menopon gallinae* (shaft louse): ***A***, Ventral view; ***B***, dorsal view; ***C***, genitalia. Redrawn with minor modification by Wen Sam Wang from Emerson (1956); courtesy of Journal of Kansas Entomological Society.

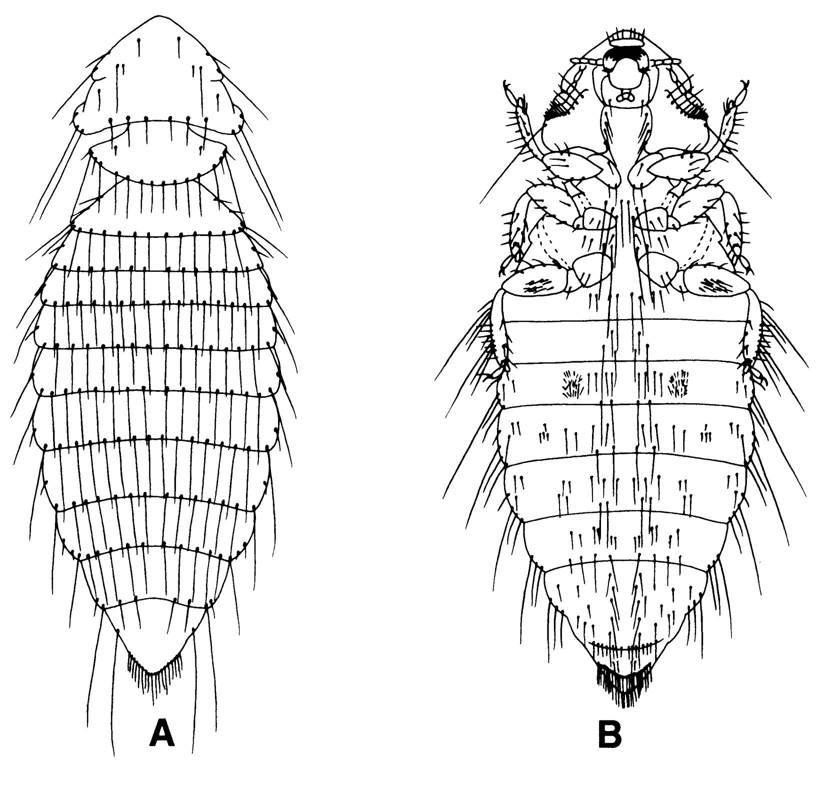


Figure 28. Female *Menopon gallinae*: ***A***, Dorsal view; ***B***, ventral view. Redrawn with minor modification by Wen Sam Wang from Emerson (1956); courtesy of Journal of Kansas Entomological Society.

Genus *Neocolpocephalum*

The poorly known *Neocolpocephalum cucullare*, a parasite of the secretary bird (*Sagittarius serpentarius*), was redescribed by Martin-Mateo and Gallego (1992) from specimens collected at the Barcelona Zoo in Spain.

Genus *Eomenopon*

The genus *Eomenopon* has been revised, and 16 species are now recognized (Price and Palma 1992). All are parasites of parrots. *Eomenopon greeni* has been collected from the swift parrot, *Lathamus discolor*, in Tasmania. The swift parrot was placed in Psittacidae by American ornithologists, but Condon (1975), an Australian, placed it in the monotypic Lathaminae of the family Platyceridae.

FAMILY RICINIDAE

Three genera of Ricinidae are currently recognized (Emerson 1972b). *Ricinus* is the genus with the most species, which parasitize passerine birds worldwide. The other two genera, *Trochiloecetes* and *Trochiliphagus*, are parasites of hummingbirds in the New World. Nelson (1972) listed 38 valid species of *Ricinus* from the New World, of which 29 occur in North America north of Mexico (Emerson 1972b). Lonc (1990b) prepared a phenetic classification of 56 species of *Ricinus* using 152 morphometric features. The 24 species of *Trochiloecetes* and 10–12 species of *Trochiliphagus* are primarily Neotropical (Carriker 1960), but a few have extended their distribution into the Nearctic Zoogeographical Region. Emerson (1972b) listed two species of *Trochiloecetes* and one of *Trochiliphagus* from North America north of Mexico.

Although their hosts are small, the Ricinidae are surprisingly large; several species of *Trochiliphagus* are more than 3 mm long (Carriker 1960). The number of lice on an individual bird is low. Male lice are rare; many species have been described from females alone. In the case of *Actornithophilus*, a genus of menoponid lice, Kirk (1991) found a positive relationship between host size and louse size.

The mouthparts are modified for bloodsucking (Clay 1949a, b; Nelson 1972), and some authors have stated that blood is the only food of the Ricinidae, because bits of feathers and skin have never been found in their digestive tract. They do not have labial palpi as do all other Amblycera (*C* and *D* in fig. 29), and the mandibles have pointed, often needlelike, tips well suited for piercing skin (*B* in fig. 29). Both monomorphic and dimorphic mandibles are found in the family; some authors suggest a correlation between monomorphic mandibles and the blood-feeding habit. The dorsal sclerites of the mesothorax and metathorax and the first abdominal segment are fused into a single sclerite. The head tends to be elongated, almost conical in shape, with a bluntly rounded apex (*A* in fig. 29).

Although only fragments of their life history have been reported, the life cycle of Ricinidae is similar to that of other Amblycera. It consists of an egg stage, three nymphal stages, and the sexually dimorphic adult stage. Baum (1968) found that *Ricinus elongatus* (=*R. ernstlagni*) spent an average of 9 days in the egg stage, 9 days each in the first and second nymphal stages, and 12 days as a third-instar nymph. Females produced 1 egg about every 3.5 days, and their lifetime production averaged about 12.5 eggs.

The large eggs of *Ricinus* are distinctive. They differ from those of other Mallophaga on the same host in size, shape, coloring, and especially in their unusual operculum and sculpturing (*E* in fig. 29).

Baum (1968) found that males required 2 days less for development than did females. In the laboratory, the lifespan of females was 54 days, but Baum speculated that in nature, females live about 100 days and males about 76 days.

The medical and veterinary importance of these parasites of songbirds and hummingbirds has not been studied, but their blood-feeding habit suggests that they may be vectors of avian diseases.

FAMILY TRIMENOPONIDAE

The 11 species of Trimenoponidae are distributed in 6 genera (Kéler 1971, Mendez 1971, Emerson and Price 1985). All are parasites of either rodents or marsupials in Central and South America. The family is distinguished from other Amblycera by the reduced tergum 1 (in both length and width), the reduced or absent pleurite 1, the presence of five pair of abdominal spiracles that open on lateral plates, and the presence of four sensilla that open to the exterior from a single cavity (fig. 30) on the terminal segment of a four-segmented antenna (Clay 1970).

Trimenopon hispidum (fig. 31) is the only species of Trimenoponidae that occurs outside the Neotropical Zoogeographical Region. This louse has been carried on its best known host, the guinea pig (*Cavia porcellus*), to numerous countries, and it is now distributed worldwide. *T. hispidum* has also been collected from wild specimens of *C. porcellus* and five other species of *Cavia* in South America (Kéler 1971, Emerson and Price 1975). It is a small louse, about 1.25 mm long, and is rarely seen in modern guinea pig colonies (Ronald and Wagner 1976). Almost nothing is known about its life history and host relationships.

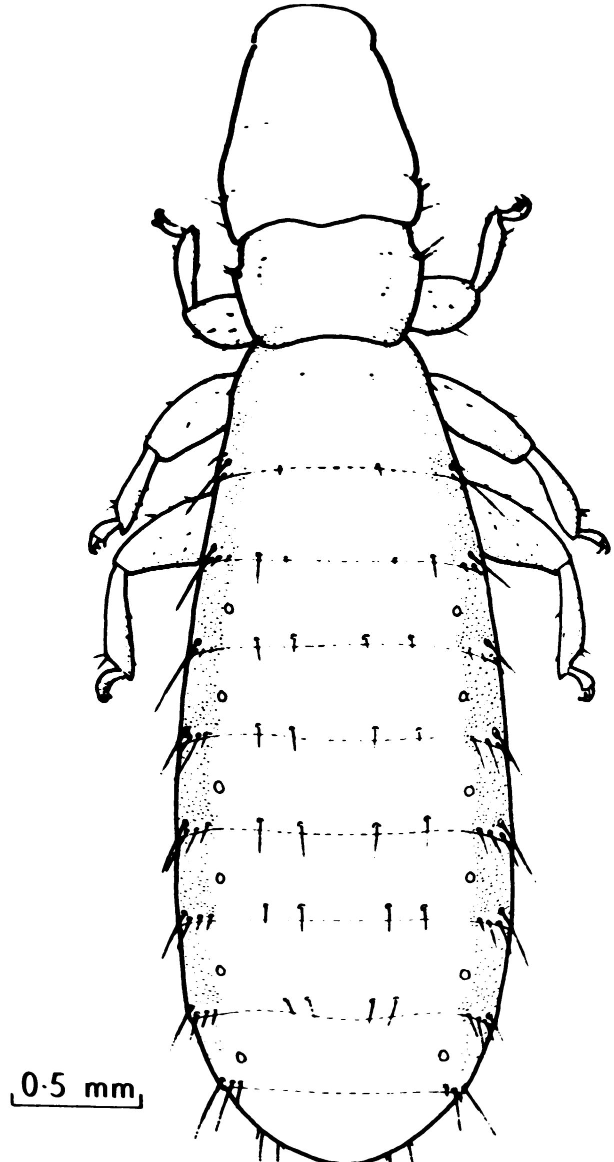
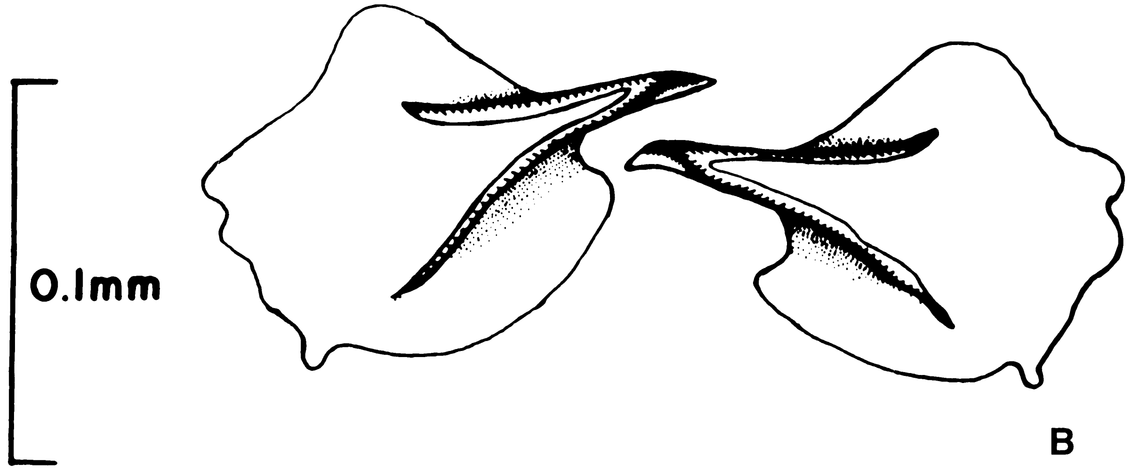
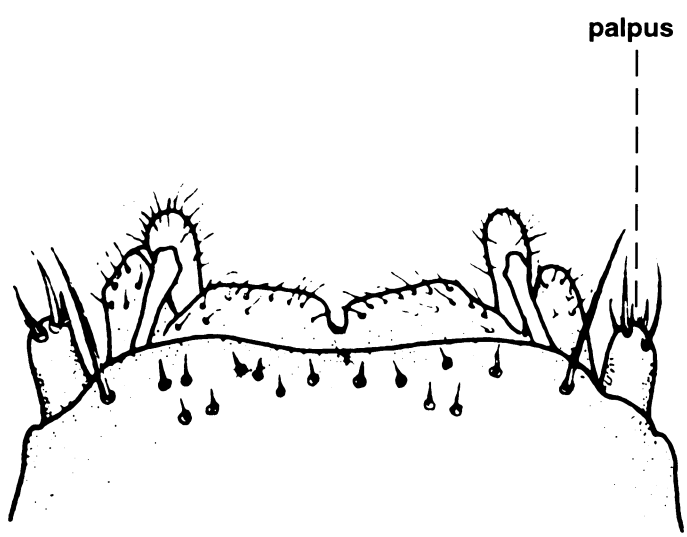


Figure 29. Morphological characteristics of the Ricinidae. ***A***, Note shape of almost conical head of *Ricinus elongatus* (=*R. ernstlangi)*. (See **B–E** on following pages.)

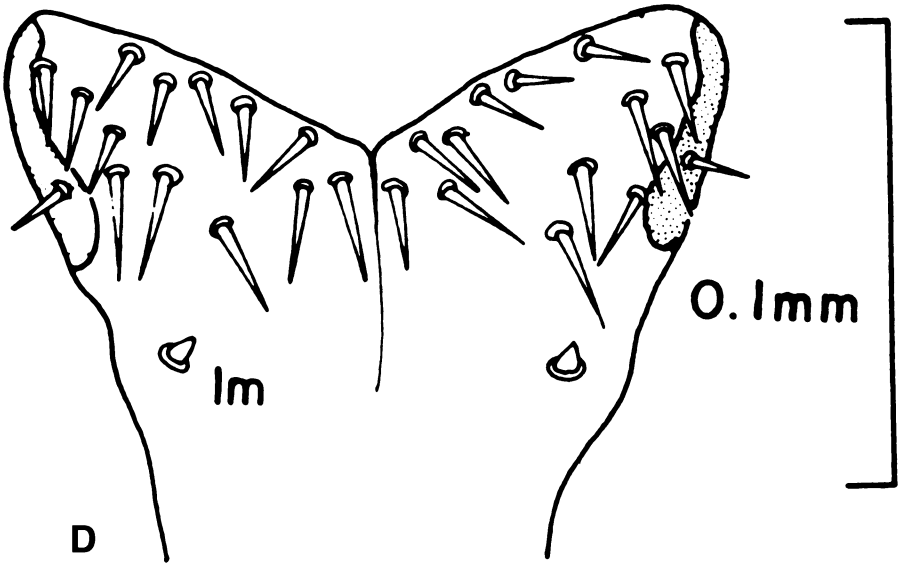


B



C

Figure 29–Continued. Morphological characteristics of the Ricinidae. ***B***, Mandibles of *Ricinus sciuru* have sharply pointed, almost needlelike tips. ***C***, As in all Amblycera except Ricinidae, labial palpi are present in *Laemobothrion*.



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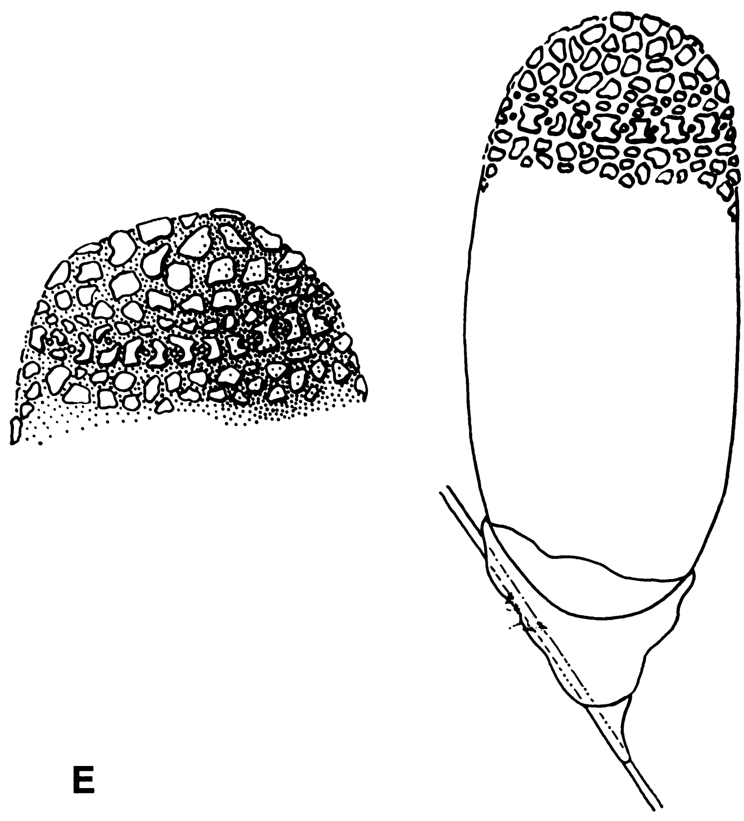


E

Figure 29–Continued. Morphological characteristics of the Ricinidae. ***D***, As in all Ricinidae, labial palpi are absent in *Ricinus sciuri*. ***E***, Egg of *Ricinus picturatus* has distinctive sculpturing. *A* and *C* from Calaby (1970), reprinted by permission of Melbourne University Press; *C* also from Snodgrass (1905); *B* and *D* from Nelson (1972), reprinted by permission of University of California Publications in Entomology; *E* from Foster (1969), reprinted by permission of Journal of Parasitology.

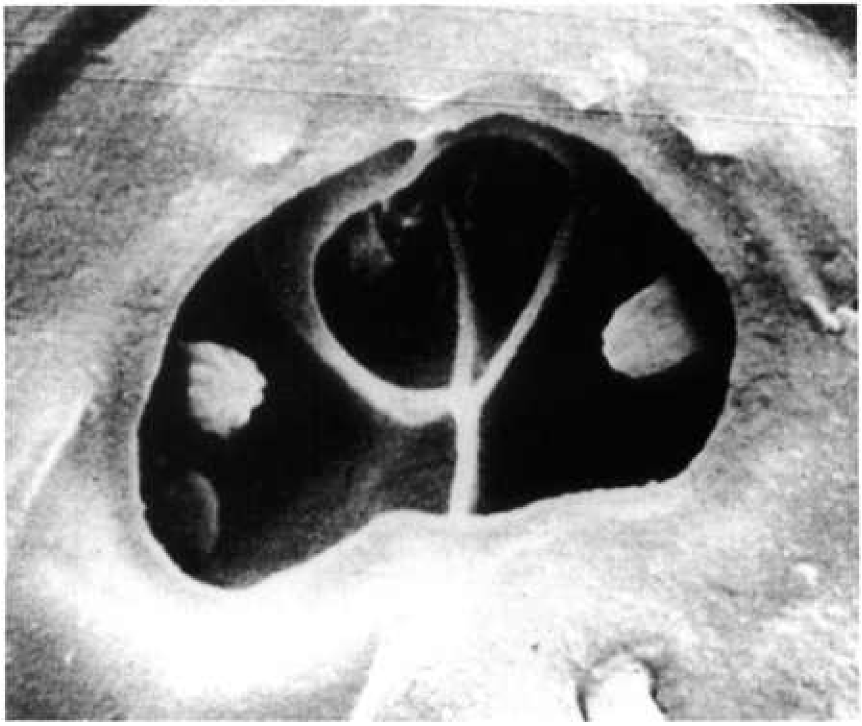


Figure 30. Antennal sense organ of *Harrisonia* sp., family Trimenoponidae. SEM × 5,373. From Clay (1970), reprinted by permission of publisher. © British Museum (Natural History), 1970.

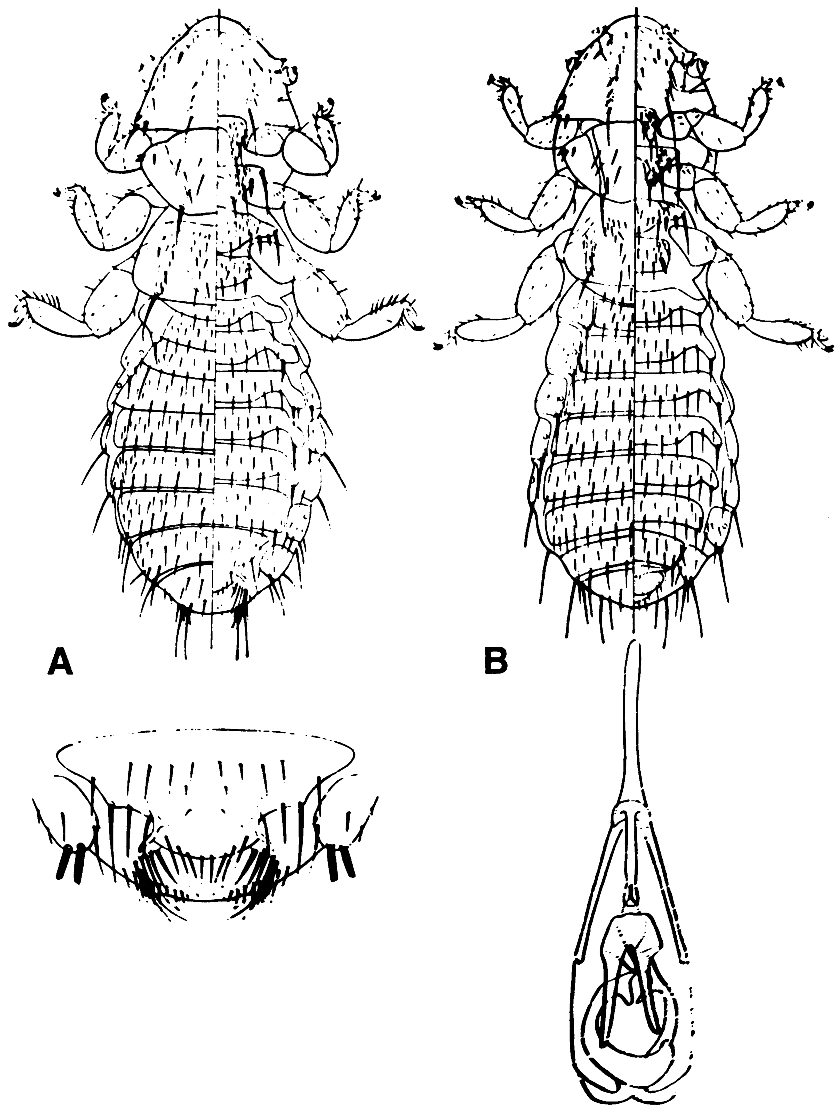


Figure 31. *Trimenopon hispidum*: ***A***, Dorsoventral view of adult female, female terminalia; ***B***, dorsoventral view of adult male, male genitalia. From Emerson and Price (1975); courtesy of Brigham Young University Science Bulletin, Biological Series.

SUBORDER ISCHNOCERA

The antennae of the suborder Ischnocera are filiform, fully exposed (figs. 32, *A* in 33), and three- or five-segmented. The mandibles are attached at more or less a right angle to the head and move in a vertical plane. The maxillary palpi are absent. The mesothorax and metathorax are fused to form a single segment, which is the pterothorax (Kettle 1984).

The Ischnocera are believed to be evolutionarily less primitive than the Amblycera (Webb 1946; Clay 1949b, 1970; Hopkins 1949; Symmons 1952; Askew 1971; Butler 1985). Bedford (1932b) contended that the opposite was true because Ischnocera lack a special groove to protect the antennae and do not have the comblike patches of setae on the ventral surfaces of the legs and abdomen that are found in certain genera of Amblycera. But his opinion was effectively refuted by others. Hopkins argued that the presence of maxillary palpi in Amblycera indicated their closer relationship to a primitive ancestor. Symmons considered the reduction of the tentorial bridge to a delicate ligament in Ischnocera to be further evidence of the loss of primitive characters. Clay found that the antennal sense organs of Ischnocera are more specialized than those of Amblycera.

Taxonomists universally recognize the division of Ischnocera into two principal families: Philopteridae (parasites of birds) and Trichodectidae (parasites of mammals). The status of two other families is less certain. The monotypic family Trichophilopteridae was established by Mjöberg (1919) for *Trichophilopterus babakotophilus* (a parasite of lemurs on Madagascar) (figs. 32, 33) and was recognized by Ewing (1929). Ferris (1933) returned *Trichophilopterus* to Philopteridae, but Marshall (1981) and Emerson and Price (1985) considered the genus sufficiently unique to justify its placement in a separate family.

The family Heptapsogastridae was established by Carriker (1936) for the Ischnocera of the Tinamiformes, a neotropical order of weak-billed, quaillike birds. Hopkins and Clay (1952) included Heptapsogastridae in their checklist but reduced the number of genera from 30 to 17. In her 1957 paper, Clay placed all avian Ischnocera in one family, Philopteridae, but referred to the *Heptapsogaster*-complex with 25 described genera, a number that she suggested would be reduced to 15 or less. Neither the lice nor their hosts were included in Emerson's (1972a,d) checklists of the Mallophaga of North America north of Mexico.

The generic category is used for grouping similar species that have a common phylogenetic origin. Clay (1951) was critical of those who established a new genus for a group of species morphologically indistinguishable from another group merely because they parasitize a distinct host group. In her opinion it was preferable to keep the generic divisions fairly wide (= large genera) to include as many related forms within the same genus as possible.

FAMILY PHILOPTERIDAE

The Philopteridae are more highly specialized than Amblycera that parasitize birds. According to Clay (1949b), many of the genera may be divided into recognizable species groups. Also, in many avian orders, the species found on a single host may be classified according to the morphological types that occupy different ecological niches on the host's body (fig. 34). The head and neck of birds are usually occupied by a short, round-bodied louse that is not greatly flattened, and these lice usually have rather large heads because of their large mandibles and strong, supportive mandibular frameworks. On the longer and broader feathers of the host's back and wings, a slender, flattened louse is usually found, which can move sideways very rapidly across broad feathers.

In contrast to Amblycera, the Philopteridae seldom move about on the host's skin; instead they remain immobile on the plumage, often attached to a feather with their mandibles. Philopteridae are less likely to abandon a dead host than are Amblycera.

The Philopteridae have five-segmented antennae and paired claws. Cope (1940) has described and illustrated in considerable detail the morphology of *Paraclisis diomedeae* (=*Esthiopterum diomedeae*), a parasite of the black-browed albatross and other albatrosses (Procellariiformes: Diomedeidae) that are representative of the family.

The feeding habits of Philopteridae also differ from those of the bird-inhabiting Amblycera. The Philopteridae use more particulate food, and blood is seldom seen in the gut. Most species feed primarily on barbs and barbules, but the wing lice feed mainly on the hooklets of feathers. These lice are believed to rely heavily on enzymes and symbionts for assistance in the digestion of their highly keratinous diet.

Philopteridae is by far the largest family of Mallophaga. Marshall (1981) calculated that more than half (1,460 of 2,590) of the species in the order have been placed in this family. Butler (1985) mentioned 98 genera, presumably worldwide. In North America, 61 genera and 633 species and subspecies of Philopteridae are known (Kim et al. 1990). Almost all orders of birds are parasitized by at least one philopterid genus, and the large orders of birds are hosts of numerous genera and species. Several species are widely distributed and are economically

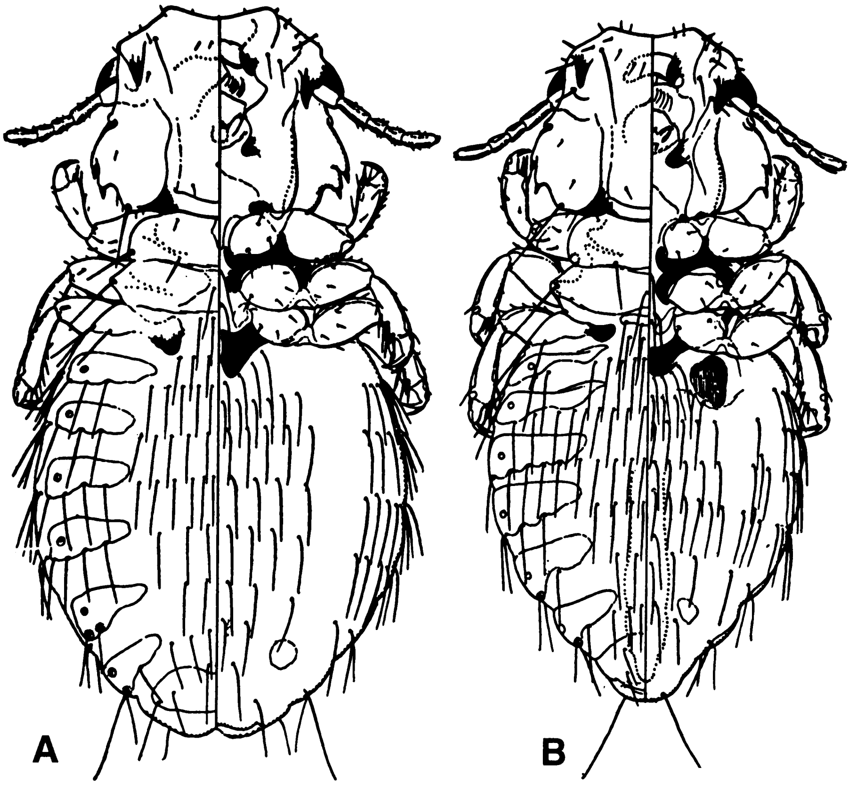


Figure 32. *Trichophilopterus babakotophilus*: ***A***, Dorsoventral view of female; ***B***, dorsoventral view of male. From Ferris (1933), reprinted by permission of Cambridge University Press.

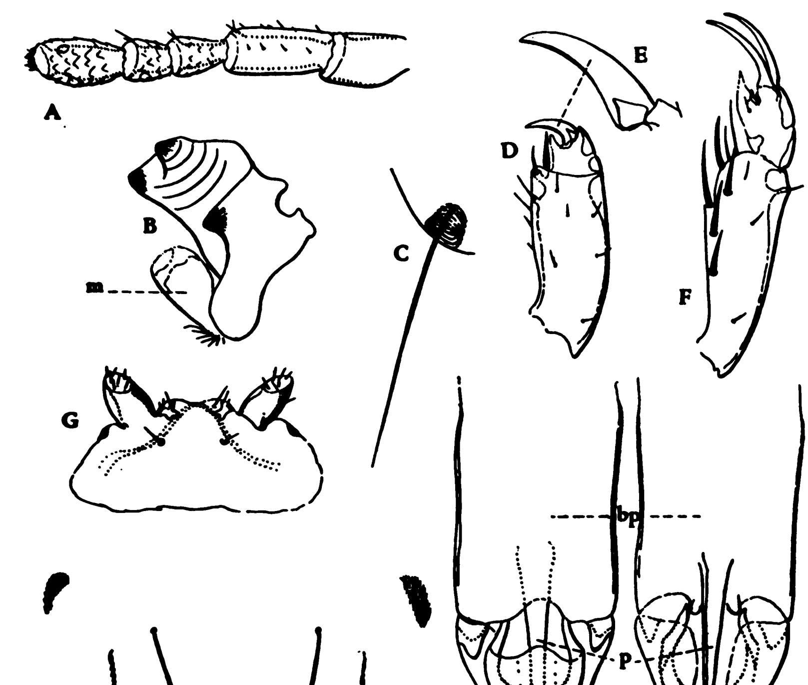


Figure 33. Taxonomic details of *Trichophilopterus babakotophilus*. ***A***, Antenna; ***B***, dorsal view of right mandible with maxilla (m); ***C***, sensory seta; ***D***, anterior tibiotarsus; ***E***, anterior claw; ***F***, posterior tibiotarsus; ***G***, labium; ***H***, female terminalia; ***I***, ventral view of male genitalia; ***J***, dorsal view of same. From Ferris (1933), Parasitology, reprinted by permission of Cambridge University Press.

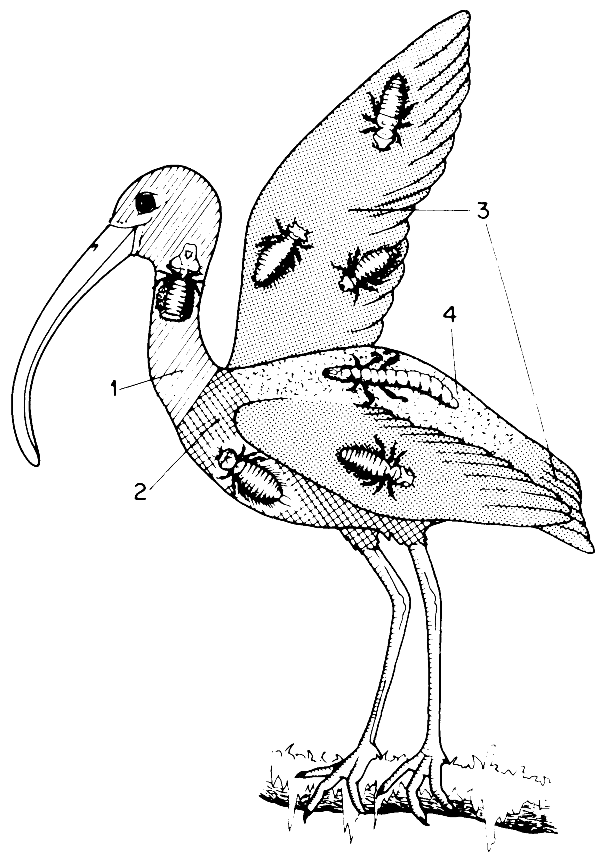


Figure 34. Ecological niches occupied by different species of bird lice on same host. From Askew (1971), Parasitic Insects, reprinted by permission of author.

important parasites of poultry (discussed more fully below).

Genus *Cuclotogaster*

At the time that he described *Cuclotogaster* as a new genus, Carriker (1936) remarked that it appeared to be more closely related to *Lipeurus* than to other genera in the family. His *Cuclotogaster laticorpus* was the only species in the new genus, but Hopkins and Clay (1952) added 25 others and listed Carriker's *C. laticorpus* as a synonymn of *Cuclotogaster heterographus*. The other species in the genus are parasites of Old World chukars, partridges, and related gallinaceous birds.

Emerson (1972a) listed only three species from North America—all introduced. *Cuclotogaster heterogrammicus* parasitizes the gray partridge (*Perdix perdix*), *C. obscurior* is from the chukar (*Alectoris graeca chukar*) (Sibley and Monroe 1990), and *C. heterographus* is a cosmopolitan parasite of domestic chickens. Martin-Mateo (1990) elevated *C. barbara*, a parasite of *Alectoris barbara* in the Canary Islands, from a subspecies of *C. heterographus* (Clay 1938a) to species rank and provided a complete description of *C. barbara*.

Cuclotogaster heterographus (chicken head louse)

The thorax of *Cuclotogaster heterographus*, the chicken head louse, is shorter and wider and the abdomen is larger and more oval than those of *Lipeurus* (compare figs. 35 and 36 with figs. 48 and 49). Probably *C. heterographus* was originally a parasite of Mediterranean partridges that transferred to the domestic chicken and spread worldwide with the new host.

Life history. In vitro rearing studies reported by Wilson (1934), Bair (1950), Conci (1952), and Stenram (1956) provided some information about the life history of the chicken head louse. When maintained at 34–36 °C (which Wilson decided was about optimum), the eggs hatched in 5–7 days. The nymphal developmental periods were 6–14 days for the first instar, 8–14 days for the second instar, and 11–14 days for the third-instar nymph. Wilson found that the life cycle from egg to adult was completed in 32–36 days. Bair concluded that a higher temperature, 42.9 °C±0.34°, was selected by lice that were free to move to higher or lower temperatures. He pointed out that the average skin temperature of a chicken's head and neck is 41.5 °C. Bishopp and Wood (1917b) simply stated that eggs of the chicken head louse hatch in 4–5 days and that nymphal development requires another 17–20 days.

Wilson (1934) observed that during copulation the male louse positioned itself under the female so that she was on his back and then grasped her abdomen with his antennae (other writers say that the male clasps the female in front of the third coxae). The tip of the male abdomen was then bent up until it entered the tip of the female abdomen, and this act was followed by insemination. Eggs are deposited singly on the down or small feathers on the chicken's head (fig. 37).

Host-parasite relationships and economic importance. Although best known as a pest of domestic chickens, *Cuclotogaster heterographus* has been reported from ring-necked pheasants, guinea fowl, and other birds if raised in close association with chickens. Subspecies other than the typical have been reported from chukars and other partridges in Asia Minor and North Africa (Clay 1938a). Reportedly, the chicken head louse has sometimes been abundant on young ducks that had been hatched under a hen (Bishopp and Wood 1917b).

On chickens, *C. heterographus* is most often found near the base of feathers on the head and neck (Price et al. 1969), but on heavily infested hosts it may spread to other body regions. This louse feeds on barbules on the fluffier part of the feather (fig. 38) by cutting the barbules into short lengths and then using the front legs to push the bits through the space between the mandibles (Wilson 1934) and into the hypopharynx. When chickens are heavily infested, the chicken head louse irritates the host and may cause severe restlessness and debility (Kim et al. 1973). Chicks are more susceptible to injury than are older birds, apparently because the lice thrive in the down on a baby chick; sometimes chicks are killed by this louse (Loomis 1978).

Genus *Goniocotes*

Six species of *Goniocotes* are known from North America; all are assumed to have been introduced along with their hosts (Emerson 1972a). It is estimated that 34 species occur worldwide. The hosts are Old World gallinaceous birds. As a group, the *Goniocotes* are smaller than the similar genus *Goniodes*.

Goniocotes gallinae (=*hologaster*) (fluff louse)

Distribution of *Goniocotes gallinae* is worldwide; the domestic chicken is the type host, but the species has also been collected from wild chickens in Thailand, Laos, and the Philippine Islands (Emerson and Elbel 1957a).

G. gallinae can be separated from other Mallophaga of poultry by the presence of two long setae on the posterior margin of the head and by the lateral margins of the prothorax being extended (Sanders 1960). The pale-yellow, sluggish fluff louse is the smallest of the poultry lice and is so broad that it appears almost circular (figs. 39, 40).

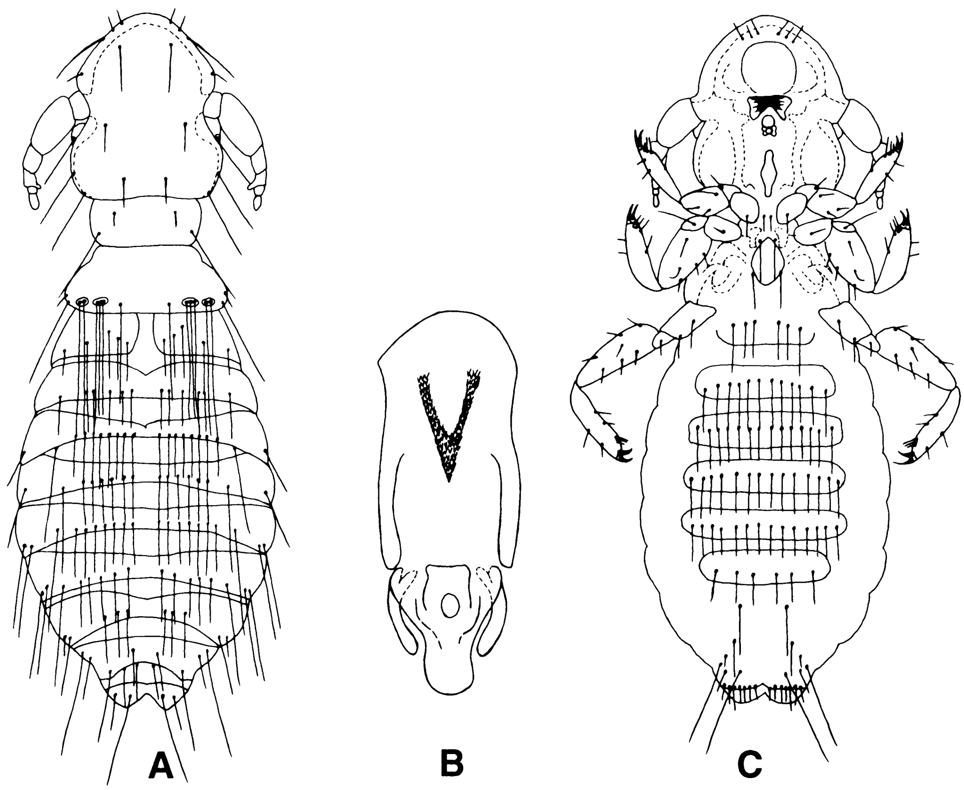


Figure 35. Male *Cuclotogaster heterographus* (chicken head louse): ***A***, Dorsal view; ***B***, genitalia; ***C***, ventral view. Redrawn with minor modification by Wen Sam Wang from Emerson (1956); courtesy of Journal of Kansas Entomological Society.

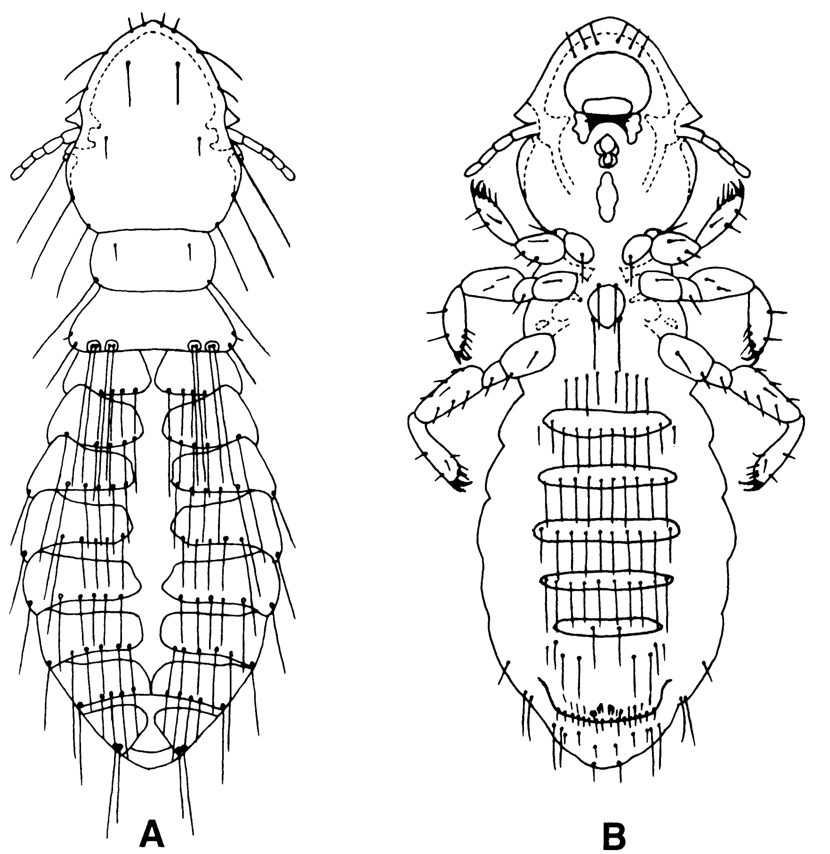


Figure 36. Female *Cuclotogaster heterographus*: ***A***, Dorsal view; ***B***, ventral view. Redrawn with minor modification by Wen Sam Wang from Emerson (1956); courtesy of Journal of Kansas Entomological Society.

Figure 37. Eggs of *Cuclotogaster heterographus* on a chicken feather. From Bishopp and Wood (1917b), U.S. Department of Agriculture.

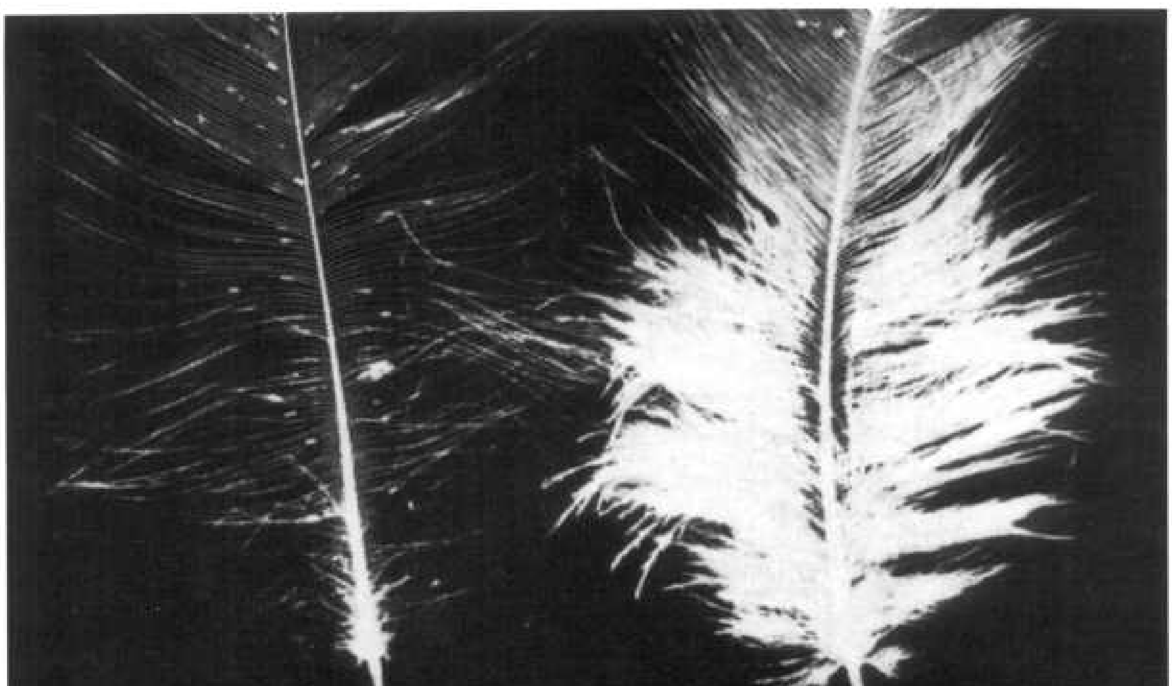


Figure 38. Chicken feather on left has been damaged by the feeding of *Cuclotogaster heterographus*. Feather on right is undamaged. From Wilson (1934), reprinted by permission of Journal of Parasitology.

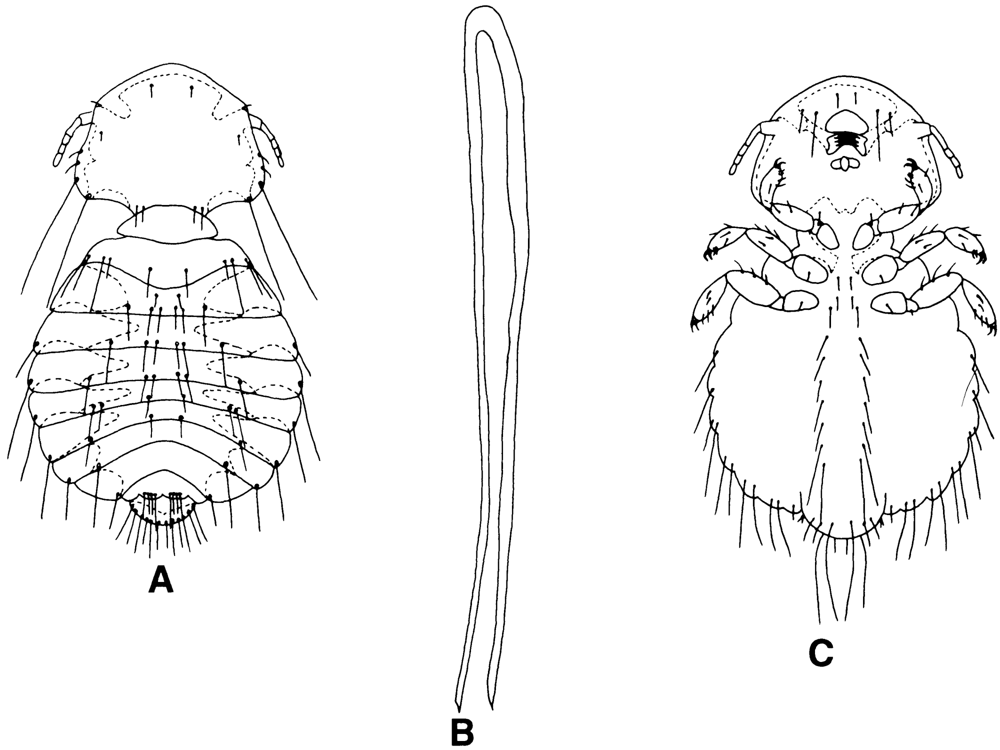


Figure 39. Male *Goniocotes gallinae* (fluff louse): ***A***, Dorsal view; ***B***, genitalia; ***C***, ventral view. Redrawn with minor modification by Wen Sam Wang from Emerson (1956); courtesy of Journal of Kansas Entomological Society.

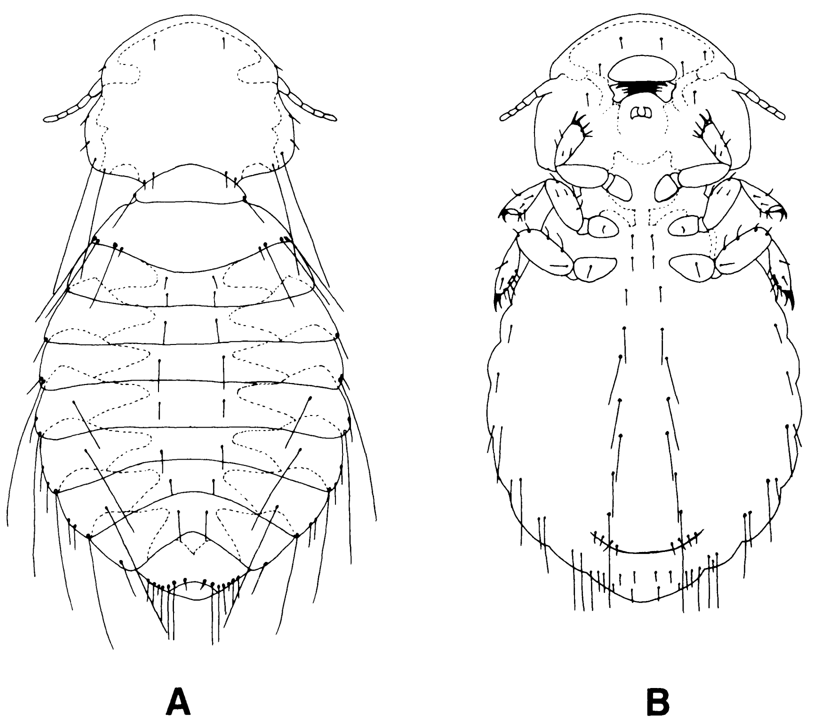


Figure 40. Female *Goniocotes gallinae*: ***A***, Dorsal view; **B**, ventral view. Redrawn with minor modification by Wen Sam Wang from Emerson (1956); courtesy of Journal of Kansas Entomological Society.

Apparently the life history of *Goniocotes gallinae* has not been studied.

The fluff louse is usually seen attached to the down or fluff at the base of feathers on the chicken's back, or around the vent, but may occur on feathers on any part of the body. Trivedi et al. (1991) found it to be fairly evenly distributed over the host, with 26% on the back, 27% on the abdomen, and lesser numbers on the breast, tail, and wings.

Although generally believed to be an economic pest of chickens, *G. gallinae* is usually considered to be less damaging than some of the other poultry lice (Roberts 1952, Roberts and Smith 1956, Furman 1962, Kim et al. 1973, Kettle 1984).

Other species of *Goniocotes*

The peafowl (*Pavo cristatus)* is a host for *Goniocotes rectangulatus* and *G. parviceps* worldwide and for *G. mayuri,* a species from the Indian subcontinent that is apparently sympatric with *G. parviceps* (Lakshminarayana and Emerson 1971, Emerson 1972a). The green peafowl (*Pavo muticus*) was added as a host of *G. parviceps* in Thailand (Emerson and Elbel 1957b). In North America, as in other places where their hosts occur, *G. microthorax* is known from the gray partridge (*Perdix perdix*) and chukar (*Alectoris graeca chukar*), *G. maculatus* from guinea fowl, and *G. chrysocephalus* from the ring-necked pheasant (*Phasianus colchicus*).

Genus *Goniodes*

The *Goniodes* are cosmopolitan parasites of gallinaceous birds. This rather large genus contains approximately 79 species worldwide (Clay 1940; Emerson 1950a; Hopkins and Clay 1952, 1953, 1955), and Emerson (1972a) listed 20 species from North America. *Goniodes* and *Goniocotes* are closely related; historically, certain species have been moved back and forth between the two genera. *Goniodes* are usually considerably larger than *Goniocotes* and have a head that is broadly rounded anteriorly and bears a broad transverse stripe or band. The postantennal region of the *Goniodes* head has more than two long setae, and the head also has other long setae on the dorsum. The temporal angle of the head has a lateroventral process that bears a small hair or spine in at least one sex and usually in both. The posterolateral margin of the prothorax is rounded, not angular. The pterothorax does not have any indication on the sides that it is divided by a meso-metathoracic suture, and it always bears a fine ventrolateral hair arising from a pit in the integument.

Goniodes gigas (large chicken louse)

Apparently *Goniodes gigas* (figs. 41, 42) was carried to all parts of the world on its type host, guinea fowl, but it is now a cosmopolitan parasite of chickens. It is the largest of the chicken lice; females average 4.2 mm and males 3.3 mm in length. It is separated from other *Goniodes* on chickens in that it has three long setae on each temporal lobe and does not have sexually dimorphic antennae. The large chicken louse is more prevalent in the Tropics than in temperate climates (Kim et al. 1973).

By observing a small laboratory colony, Conci (1956) found that at 35–38 °C the eggs of the large chicken louse hatched in about 7 days and that the life cycle was completed in about 1 mo. Maximum longevity was 19 days for males and 24 days for females. The maximum number of eggs laid by a single female was 14.

Crutchfield and Hixson (1943) found only feather barbs and barbules in the crop contents of the large chicken louse and concluded that those were the sole food.

Although it is large, *G. gigas* seems to be usually present in small numbers and it is therefore less injurious to its host than are some of the other poultry lice. Distribution on the host was studied by Trivedi et al. (1991), who reported that over half of the lice were localized on the chicken's back. In South Africa, *G. gigas* was usually present on wild guinea fowl and was one of the three most abundant louse species (Louw et al. 1993).

Goniodes dissimilis (brown chicken louse)

The reddish-brown *Goniodes dissimilis* is similar to *G. gigas* but is distinguished by its smaller size (females average 2.98 mm and males 2.36 mm in length), the thick clypeal band in both sexes, the sexually dimorphic antennae, and only two long setae on each temporal lobe (figs. 43, 44) (Clay 1940, Emerson 1956). The brown chicken louse is a widely distributed parasite of domestic chickens, but its true host is probably the wild chicken. Although *G. dissimilis* is a common pest in temperate climates, it has never been reported as abundant on a single host, and serious injuries have never been recorded. Trivedi et al. (1991) found that the distribution of the brown chicken louse on a chicken was almost identical with the distribution of *G. gigas*.

Goniodes colchici

In both the Old and New Worlds, pheasants (various varieties of *Phasianus colchicus*) are quite commonly infested with *Goniodes colchici* (fig. 45) (Clay 1940; Emerson 1950b, 1972a,d), a species that differs from other *Goniodes* in the structure of the male and female genitalia and in abdominal chaetotaxy.

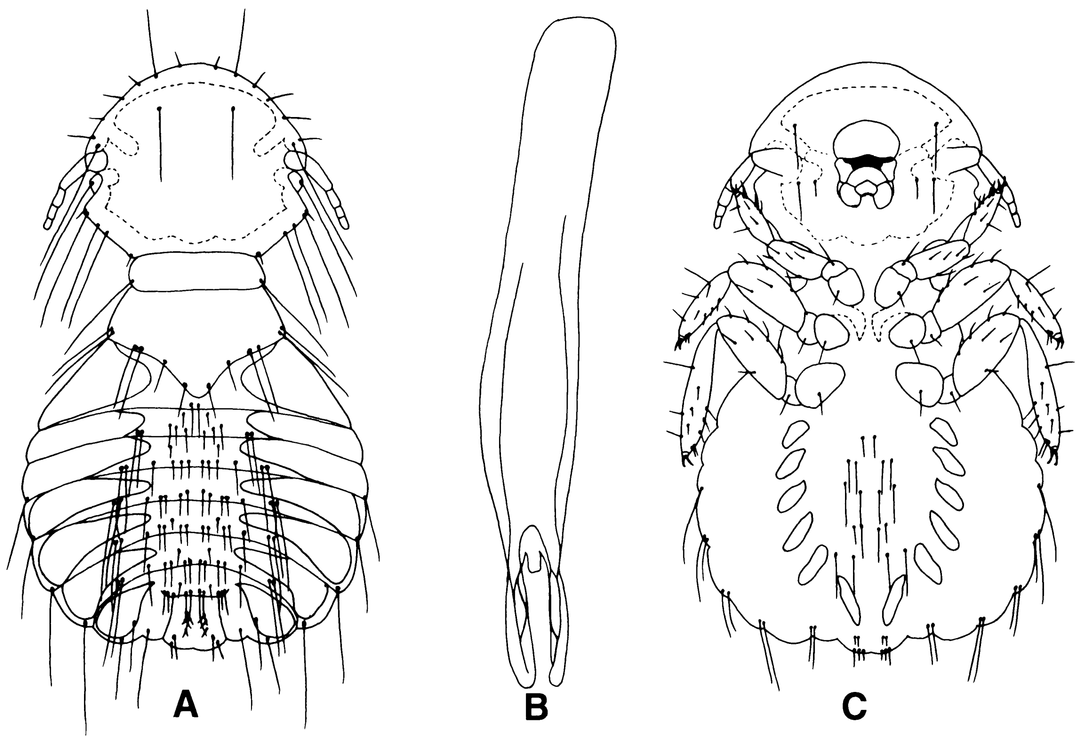


Figure 41. Male *Goniodes gigas* (large chicken louse): ***A***, Dorsal view; ***B***, genitalia; ***C***, ventral view. Redrawn with minor modification by Wen Sam Wang from Emerson (1956); courtesy of Journal of Kansas Entomological Society.

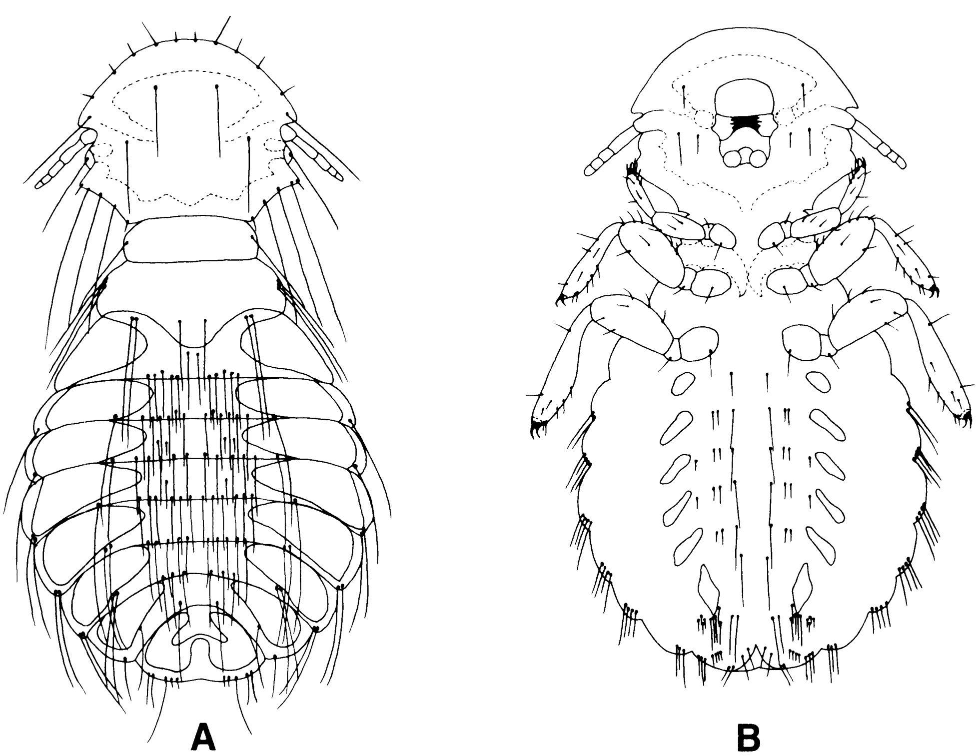
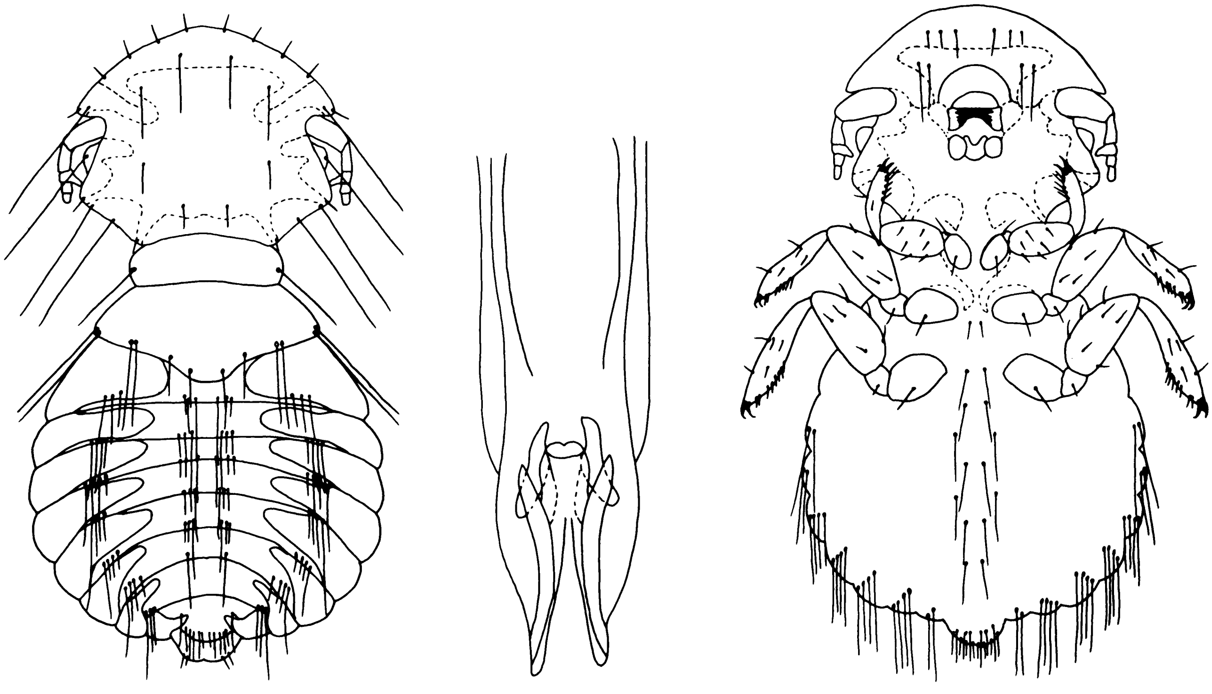
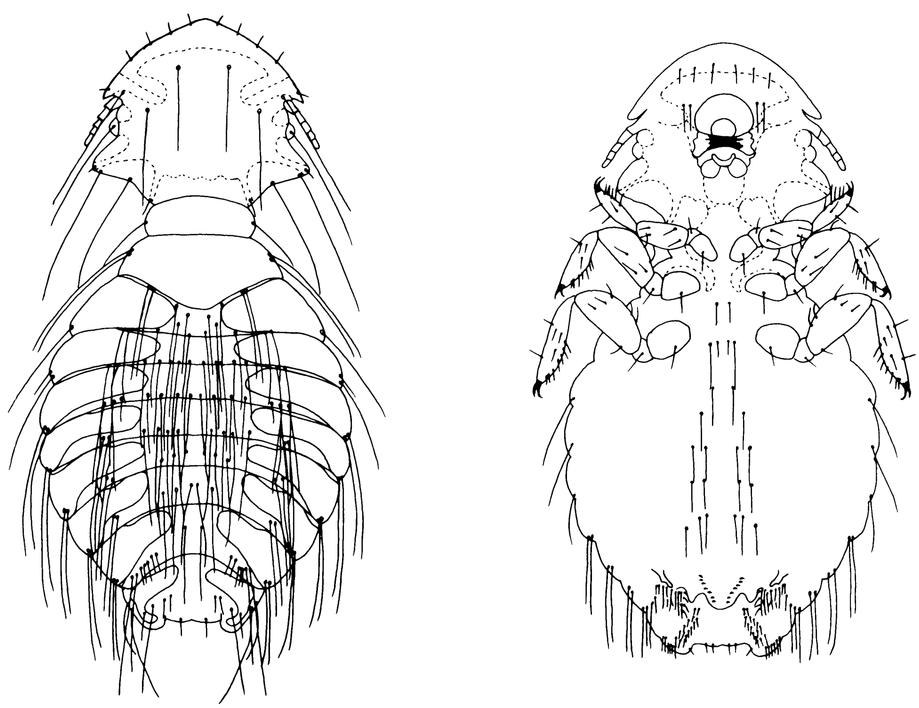


Figure 42. Female *Goniodes gigas*: ***A***, Dorsal view; ***B***, ventral view. Redrawn with minor modification by Wen Sam Wang from Emerson (1956); courtesy of Journal of Kansas Entomological Society.



A B C

Figure 43. Male *Goniodes dissimilis* (brown chicken louse): ***A***, Dorsal view; ***B***, genitalia; ***C***, ventral view. Redrawn with minor modification by Wen Sam Wang from Emerson (1956); courtesy of Journal of Kansas Entomological Society.



A B

Figure 44. Female *Goniodes dissimilis*: ***A***, Dorsal view; ***B***, ventral view. Redrawn with minor modification by Wen Sam Wang from Emerson (1956); courtesy of Journal of Kansas Entomological Society.

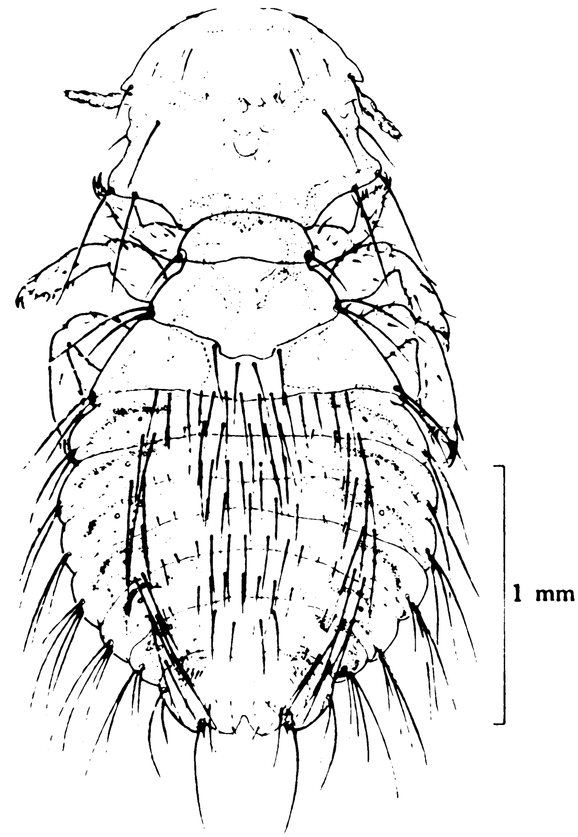


Figure 45. Female *Goniodes colchici.* From Williams (1970a), reprinted by permission of Australian Journal of Zoology.

In a series of in vitro rearing studies, Williams (1970a,b, 1971) learned that *G. colchici* is able to survive at temperatures of 30–40 °C if the relative humidity exceeds about 60%. Egg production was in part regulated by the ability of females to maintain their water balance; the most favorable temperature for water uptake was 36.8 °C. Maximum oviposition was one egg per day for females held at 35 °C and 75% relative humidity. Apparently *G. colchici* in nature is able to find its optimum microhabitat by moving up or down a feather; Williams calculated that temperatures along a pheasant's feathers ranged from about 40 °C near the skin to about 25 °C at the tip.

Nebraska was included in the distribution of *G. colchici* by Payne et al. (1990), who collected four species of Mallophaga from the ring-necked pheasant in that state. The other three species were *Lipeurus maculosus, Lagopoecus colchicus*, and *Amyrsidea megalosoma*.

Other species of *Goniodes*

The 17 species of North American *Goniodes* not discussed above are host-specific parasites of native and introduced gallinaceous birds (see list in appendix A, pp. A-13 through A-14 (Emerson 1950a, 1972a,d). Although transfer of a louse species to a bird species other than the usual host may occur when different kinds of birds are raised together, most species of *Goniodes* have only one normal host. A few exceptions are known, but in those cases the bird species are closely related; examples are *Goniodes lagopi* (an enlarged view of the fourth and fifth antennal segments is shown in fig. 46) from the willow ptarmigan (*Lagopus lagopus*) and the rock ptarmigan (*Lagopus mutus*). The white-tailed ptarmigan (*Lagopus leucurus*) has its own species of *Goniodes*: *G. leucurus.* Domestic peafowl are parasitized by *G. meinertzhageni* and *G. pavonis*, and guinea fowl are parasitized by *G. gigas* and *G. numidae.* No *Goniodes* has been reported from either wild or domestic turkeys (Emerson 1962c).

Genus *Lagopoecus*

The head and thorax of *Lagopoecus* resemble those of *Cuclotogaster*, but the male genitalia differ (Wiseman 1959). The antennae of nine North American species of *Lagopoecus* are filiform in both sexes, and a long seta arises from the dorsum of the head near the eye (Clay 1938b; Emerson 1950b, 1957).

Lagopoecus sinensis

Sugimoto (1930) described *Lagopoecus sinensis* from specimens that had been collected from the domestic chicken at Wenchow, Chekiang Province, China. Because no other specimens were collected for several years, doubts arose that chickens were the true host. However, later collections from Chinese chickens were reported by Emerson (1957), who acknowledged *L. sinensis* (fig. 47) as a parasite of domestic chickens and also made new drawings of the louse. Although it was included in his checklist (Emerson 1972a), it appears that Emerson was not certain that *L. sinensis* occurs in North America.

Other species of *Lagopoecus*

In addition to *L. sinensis*, Emerson (1972a) listed eight other species of *Lagopoecus* from North America. All are parasites of quail, pheasants, and other gallinaceous birds. Payne et al. (1990) added *Lagopoecus colchicus* to the list of ectoparasites of ring-necked pheasants (*Phasianus colchicus*) in Nebraska.

Genus *Lipeurus*

Lice in the genus *Lipeurus* are much longer than wide and have sexually dimorphic antennae. The first antennal segment of the male is enlarged with a short, thickened appendage (figs. 48, 49), and the third segment is enlarged distally. The meso-metathoracic suture is visible on the side of the pterothorax. Once *Lipeurus* occurred only in the Old World on gallinaceous birds, but the lice were carried to other regions of the world on their hosts.

Lipeurus caponis (wing louse)

The wing louse is a long, slender, gray louse about 2.5 mm long. It can be identified by the row of short setae on the posterior margin of the vulva and by the male head being widest in the preantennal region. This louse is usually inactive and is most likely to be seen attached to barbules of the wing feathers near the shaft (Bishopp and Wood 1917a, Kim et al. 1973).

Life history. In a study reported by Wilson (1939), a small number of adult wing lice were held in an incubator at 32–33 °C. Oviposition was first noted on the fourth day of adult life. An unfertilized female laid 15 eggs in 36 days, but none hatched. Mated females produced 30–35 eggs each. Eggs were laid between the barbules of large chicken feathers. The average incubation period was 5.5 days. The average number of days for nymphal development was 9.1 days for the first instar, 8.5 days for second instar, and 7.3 days for third instar. Females lived longer than males; the average longevity of female wing lice was 31 days. Because most immature lice died before reaching the adult stage, Wilson concluded that he had not provided optimum rearing conditions.

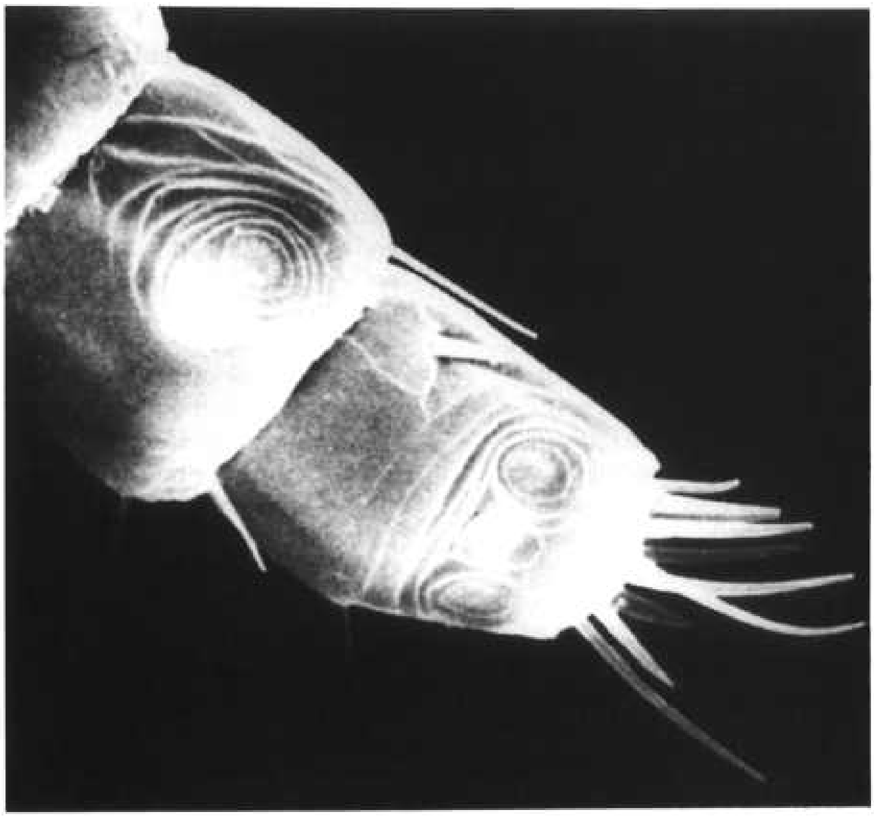


Figure 46. *Goniodes lagopi*: Fourth and fifth antennal segments with their sensilla. SEM × 667. From Clay (1970), reprinted by permission of publisher. © British Museum (Natural History), 1970.

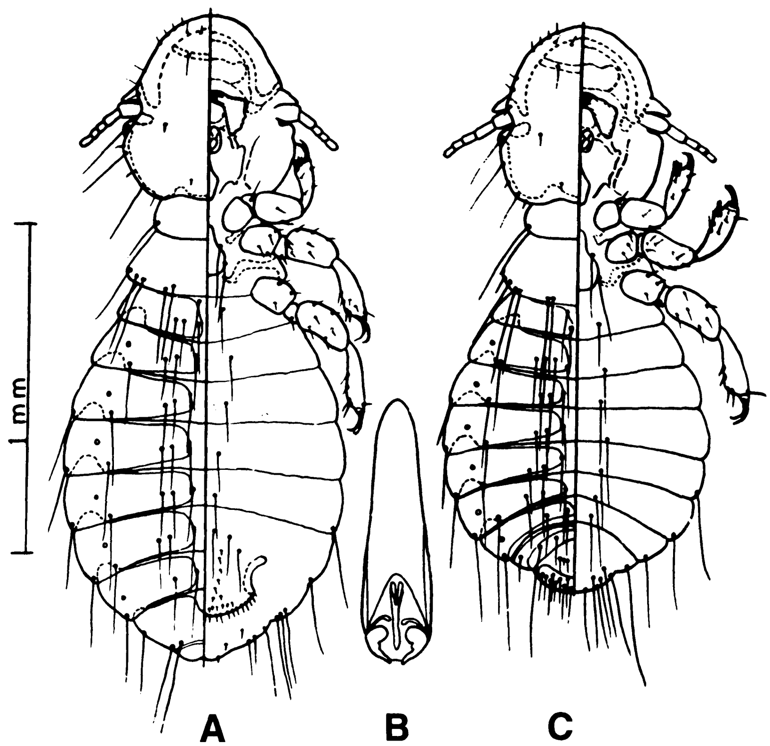


Figure 47. *Lagopoecus sinensis*: ***A***, Dorsoventral view of female; ***B***, male genitalia; ***C***, dorsoventral view of male. From Emerson (1957), reprinted by permission of Journal of Kansas Entomological Society.

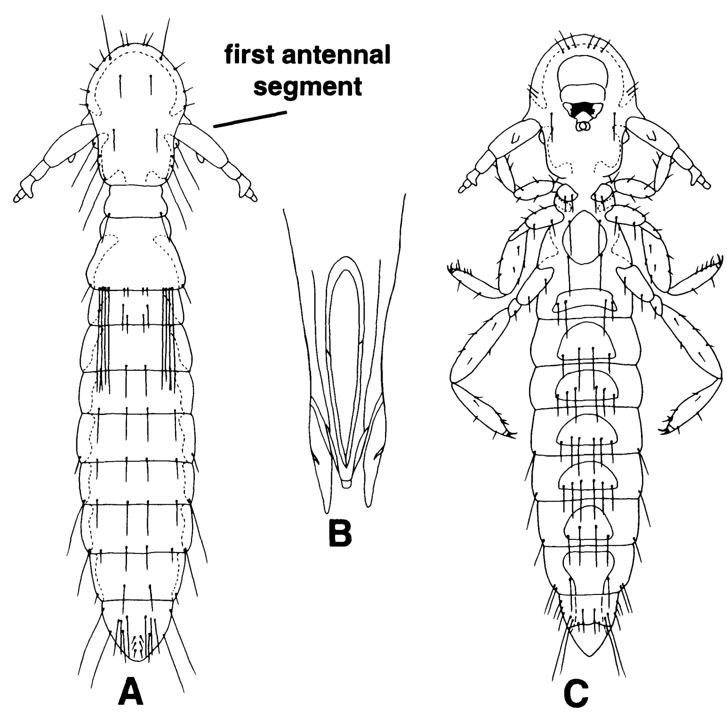


Figure 48. Male *Lipeurus caponis* (wing louse): ***A***, Dorsal view (note enlarged first antennal segment); ***B***, genitalia; ***C***, ventral view. Redrawn with minor modification by Wen Sam Wang from Emerson (1956); courtesy of Journal of Kansas Entomological Society.

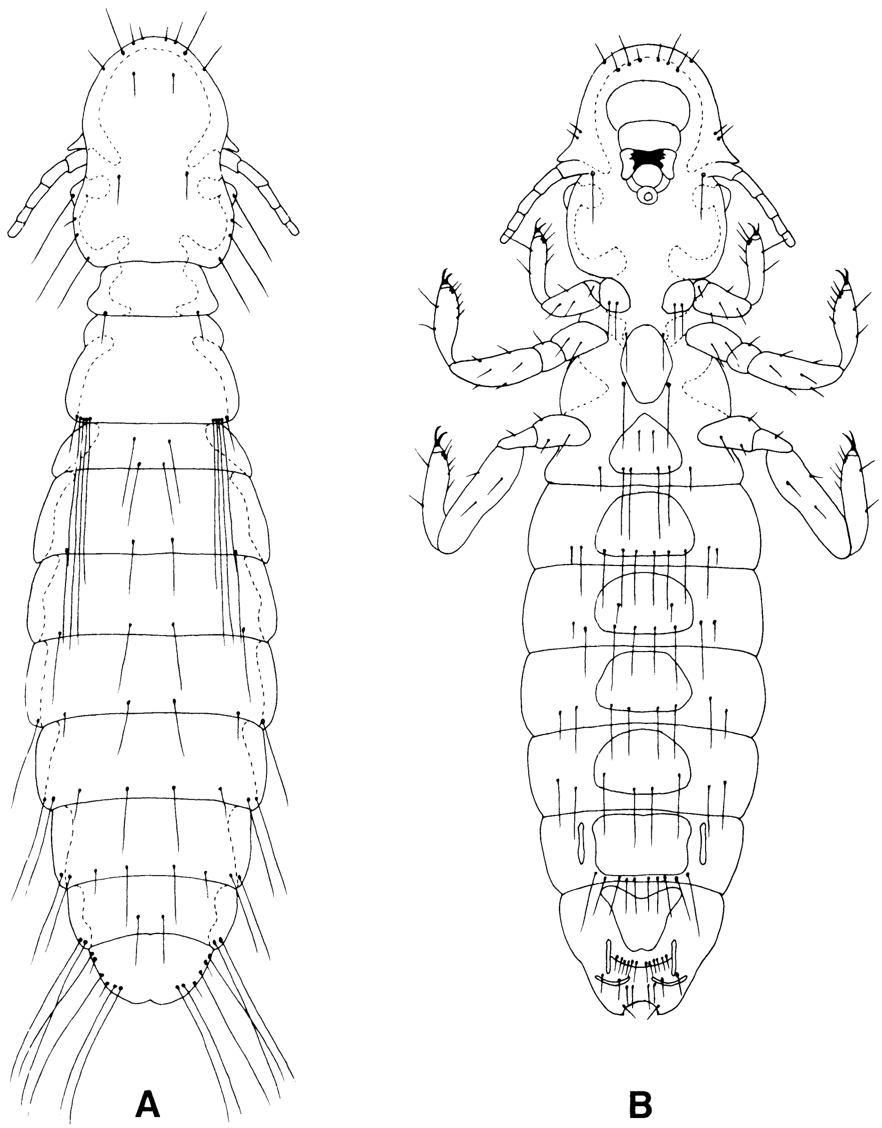


Figure 49. Female *Lipeurus caponis*: ***A***, Dorsal view; ***B***, ventral view. Redrawn with minor modification by Wen Sam Wang from Emerson (1956); courtesy of Journal of Kansas Entomological Society.

Host-parasite relationships. Crutchfield and Hixson (1943) decided that feather particles are the sole food of *Lipeurus caponis,* because the only substance found in the crops of almost all specimens examined by them was feather hooklets. Only an occasional louse had consumed pieces of barbs and barbules. The wing louse frequents the underside of the large wing feathers. Because of this louse's dark color, relatively large size, and sluggish movement, it is easily seen there, especially on white chickens (Bishopp and Wood 1917a).

Trivedi et al. (1991) found that 87% of *L. caponis* were attached to wing feathers (a few were on the neck and tail); thus it is easy to understand why the species was given the name "wing louse." Chickens are noticeably injured by the wing louse only if they are heavily infested, which apparently is rare (Kim et al. 1973). However, Maldonado-Capriles and Miro-Mercado (1978) found *L. caponis* to be more abundant than other poultry lice in a flock of 5,000 hens in Puerto Rico; they reported that those chickens were heavily infested.

Other species of *Lipeurus*

Hopkins and Clay (1952, 1953, 1955) listed 37 species of *Lipeurus* other than *L. caponis*, and Emerson (1972a) listed 3 species from North America, all from introduced birds. The ring-necked pheasant is the host of *Lipeurus maculosus*; guinea fowl have *L. numidae*, and peafowl have *L. pavo*.

Still another species, *Lipeurus lawrensis tropicalis*, had not been reported from the continental United States in 1956, but it occurred on chickens in Puerto Rico, Cuba, West Indies, and other tropical localities (Emerson 1956). The biology of *L. l. tropicalis* in northern India was described by Arora and Chopra (1957), who found that the optimum conditions for rearing it in the laboratory were 35 °C and 80%–85% relative humidity. Mating occurred 2–4 hr after adult eclosion, and females began to oviposit at the rate of 3–5 eggs/day when they were 2–3 days old. The average number of eggs was 23.

Eggs were laid singly along a barb; but because females often attach eggs near other eggs, they were arranged in a symmetrical pattern on a feather (fig. 50). The most eggs counted on a single feather was 495 (Arora and Chopra 1957).

Chickens severely infested with *Lipeurus lawrensis tropicalis* are uncomfortable and react by wallowing in dirt and attempting to free themselves of lice by scratching with their feet and beaks (Arora and Chopra 1957). The skin and plumage are often stained and discolored by the lice, and the chicken's constant scratching breaks the skin and causes it to bleed.

Trivedi et al. (1991) found that over 50% of *L. l. tropicalis* were located on the nape and neck of chickens. Under natural conditions in Banaras, India, the louse population increased to a peak in May and June following spring temperature increases but while relative humidity was still above 60% (Agarwal and Saxena 1979).

Genus *Oxylipeurus*

Oxylipeurus have slender bodies, and the chitin of the anterior band of the head is modified into a number of projections or a raised transverse line (Clay 1938a). The 69 species (Hopkins and Clay 1952, 1953, 1955) are parasites of birds in several families of Galliformes. Emerson (1972a) listed nine North American species—two from introduced birds and the others from native hosts.

Oxylipeurus dentatus

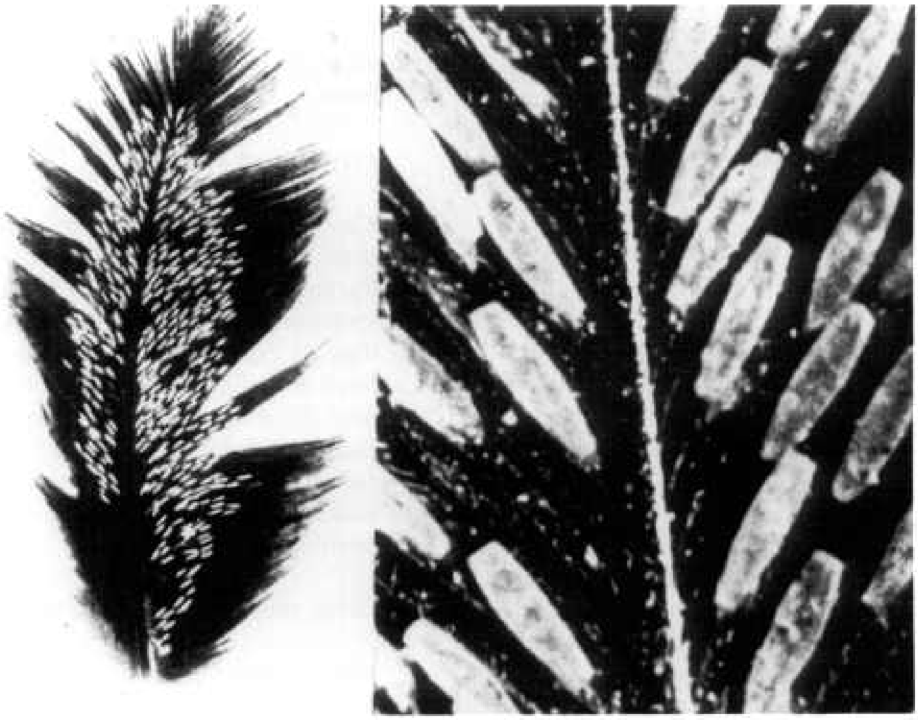
Oxylipeurus dentatus is a parasite of chickens, and its distribution includes India, Southeast Asia, Central Pacific islands, and Central America. This louse has a toothlike point on the anterior margin of a pointed head (figs. 51, 52). Emerson (1956) surmised that the natural hosts are wild chickens in Southeast Asia. Collections from domestic chickens in Panama and Nicaragua caused Emerson to state that its arrival in the Gulf Coast region of the United States should be expected. The life history and host relationships of this louse have not been reported.

Other species of *Oxylipeurus*

Among other *Oxylipeurus* from North America are *Oxylipeurus polytrapezius* (slender turkey louse), a common parasite of both domestic and wild turkeys, and *Oxylipeurus corpulentus* from wild turkeys (Emerson 1962a, Kellogg et al. 1969). Ring-necked pheasants are hosts of *Oxylipeurus mesopelios colchicus*, and the chachalaca (*Ortalis vetula*) is the host of *Oxylipeurus chiniri vetulae* (Carriker 1954). Four other species of *Oxylipeurus* are parasites of five species of North American quail (see appendix A, p. A-16).

Genus *Pectinopygus*

Several species of *Pectinopygus* are parasites of pelicans, cormorants, and other birds in the order Pelecaniformes (Green and Palma 1991, Martin-Mateo 1992a). Clay (1961) listed six species of *Pectinopygus* from pelicans and noted that each pelican species was infested with a single louse species (except that one species of *Pectinopygus* was found on two pelican species). Emerson (1972a) listed 12 North American species of *Pectinopygus* from Pelecaniformes.



A B

Figure 50. ***A***, Arrangement of *Lipeurus lawrensis tropicalis* eggs on a chicken feather; ***B***, closeup of eggs. From Arora and Chopra (1957), reprinted by permission of Punjab University Journal of Zoology, Lahore, Pakistan.

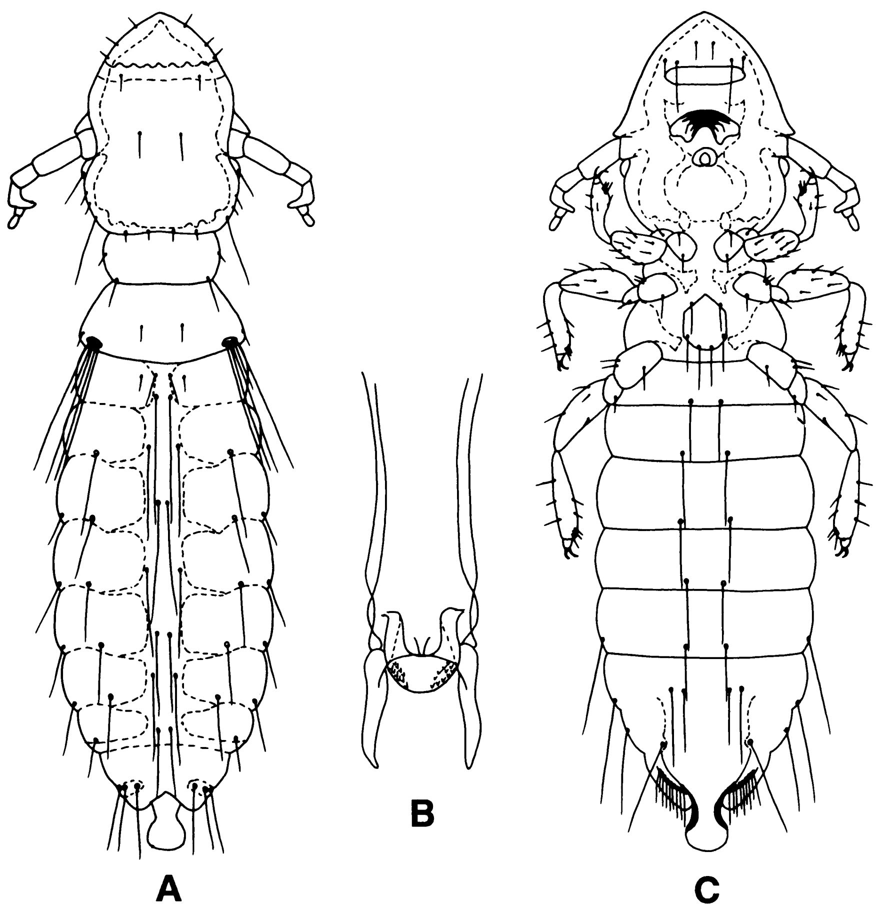


Figure 51. Male *Oxylipeurus dentatus*: ***A***, Dorsal view; ***B***, genitalia; ***C***, ventral view. Redrawn with minor modification by Wen Sam Wang from Emerson (1956); courtesy of Journal of Kansas Entomological Society.

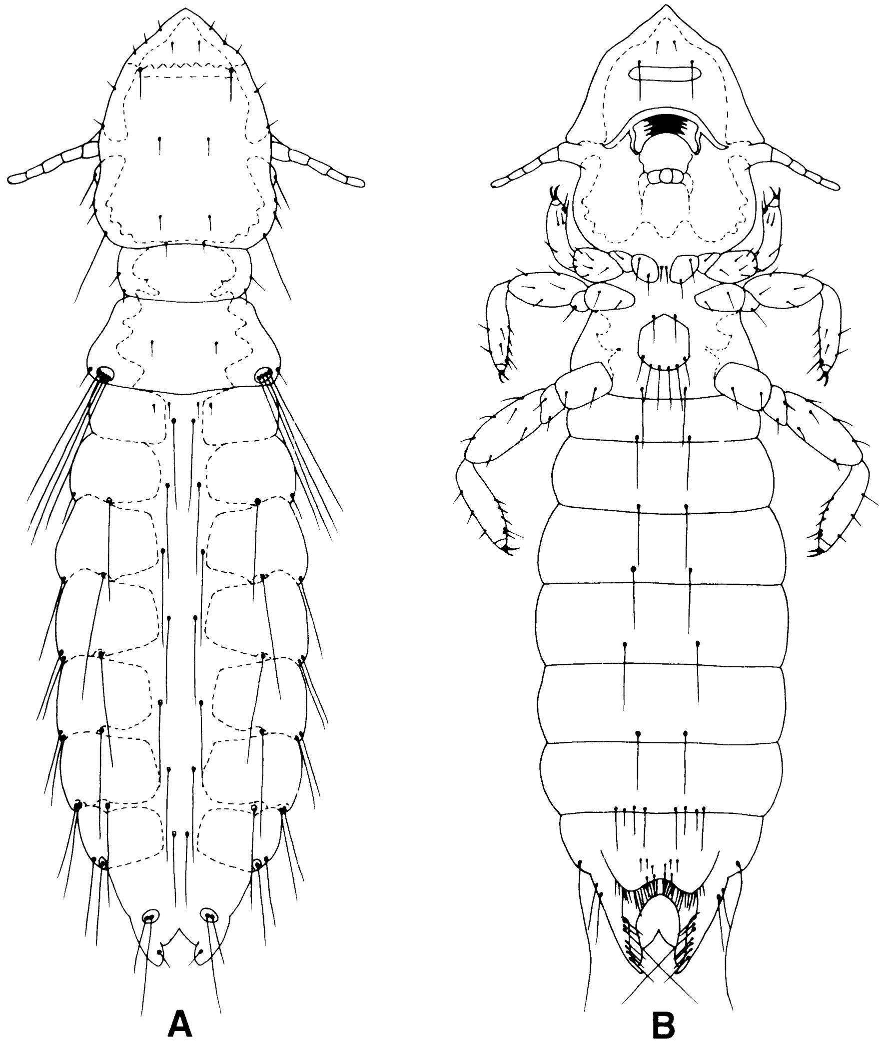


Figure 52. Female *Oxylipeurus dentatus*: ***A***, Dorsal view; ***B***, ventral view. Redrawn with minor modification by Wen Sam Wang from Emerson (1956); courtesy of Journal of Kansas Entomological Society.

Genus *Quadraceps*

Martin-Mateo (1992b) found that lice in the genus *Glareolites*, which Eichler (1944) had described from Old World pratincoles (Charadriiformes: Glareolidae), were more properly placed in *Quadraceps*. Emerson (1972a) listed 65 species and subspecies of *Quadraceps* from North American birds.

Genus *Rallicola*

The large genus *Rallicola* has been reviewed by Clay (1953, 1972) and by Emerson (1955). In his checklist of the Ischnocera of North America, Emerson (1972a) had 11 species and 3 subspecies, mostly from rails, coots, and limpkins. Three species are parasitic on kiwis; Palma (1991) described *Rallicola rodericki*, a parasite of the brown kiwi (*Apteryx australis mantelli*). Mey (1990) described a new genus and species of extinct lice, *Huiacola extinctus*, which had been recovered in museums from specimens of the extinct New Zealand huia, *Heteralocha acutirostris*. The louse is a member of the *Rallicola* complex. Price and Clayton (1993) recognized 16 species of *Rallicola* from woodcreepers (Passeriformes: Dendrolaptinae), of which 4 were newly described by them. Price and Clayton (1994) returned 10 species of *Furnaricola* to *Rallicola*.

Genus *Strigiphilus*

Although three genera of lice parasitize owls (Strigiformes), *Strigiphilus* is the only genus restricted to those birds. Clay (1966) recognized 29 species of *Strigiphilus*, and Clayton (1990a) described an additional 3 species. Within *Strigiphilus*, most of the species have been placed in the *cursitans* group; Clayton and Price (1984) redescribed 11 species of the group and placed 3 others in synonymy.

Other Genera and Species

Chelopistes meleagridis (large turkey louse)

Chelopistes are parasites of gallinaceous birds, principally in the Neotropical Zoogeographical Region (Wiseman 1959, Emerson 1960). Carriker (1945) described 26 species (plus 11 subspecies) of neotropical chewing lice and placed them in his new genus *Trichodomedea*. Hopkins and Clay (1952) synonymized *Trichodomedea* with *Chelopistes* and listed 35 valid species in the genus. Only two species of *Chelopistes* occur in North America north of Mexico (Emerson 1972a). The *Chelopistes* have sexually dimorphic antennae and an elongated abdomen, which is somewhat pointed in both sexes (fig. 53). The large turkey louse is easily recognized by its heavy sclerotization and extended temporal lobes, each with one unusually long seta.

Chelopistes meleagridis has a worldwide distribution on domestic turkeys and is a common parasite of wild turkeys. It has been collected from various varieties of the wild turkey and also from the ocellated turkey (*Agriocharis ocellata*) of southern Mexico and Central America (Clay 1941). It is most frequently found on feathers on the neck and breast of turkeys (Wiseman 1959). The life history of the large turkey louse has not been reported.

C. texanus, a parasite of the chachalaca (*Ortalis vetula*), is the only other species of *Chelopistes* from North America north of Mexico.

Falcolipeurus secretarius

A detailed redescription of this rare parasite of the secretary bird (*Sagittarius serpentarius*) (Falconiformes: Sagittariidae) was published by Martin-Mateo and Gallego (1992).

Struthiolipeurus rheae

Struthiolipeurus rheae is one of four species of Philopteridae that parasitize the common rhea (Rheiformes: Rheidae). This louse was collected from a dead bird by Weisbroth and Seelig (1974), who noted that it was infested with several thousand lice. The rhea was hatched on Long Island, New York, but the parents of the dead bird had been captured in Argentina about 3 yr earlier.

Campanulotes bidentatus compar (small pigeon louse)

The genus *Campanulotes* was erected by Kéler (1939), who used *Goniocotes compar* as the genotype. The five species of *Campanulotes* listed by Hopkins and Clay (1952) are all found on columbiform birds (pigeons and doves). The antennae are filiform in both sexes, and the angulate temporal lobes each bear two long setae. But the bell-shaped head, which the generic name describes, is the most distinctive characteristic. Although the other species of *Campanulotes* are found only in the Old World, the small pigeon louse occurs worldwide wherever the domestic pigeon has been introduced. Two subspecies of *Campanulotes bidentatus* were recognized by Hopkins and Clay—the typical one and *compar*—but the two differ only in size (Martin-Mateo 1975). Hill and Tuff (1978) regarded *compar* as a valid species, not a subspecies of *C. bidentatus*, but others (for example, Clayton 1990b) continue to use the combination *Campanulotes bidentatus compar*.

Nelson and Murray (1971) were unable to maintain an in vitro colony of the small pigeon louse but did report their observations on louse distribution on pigeons. Female lice laid eggs on most body feathers and only rarely on feathers on the head, tail, and legs. On a 17–

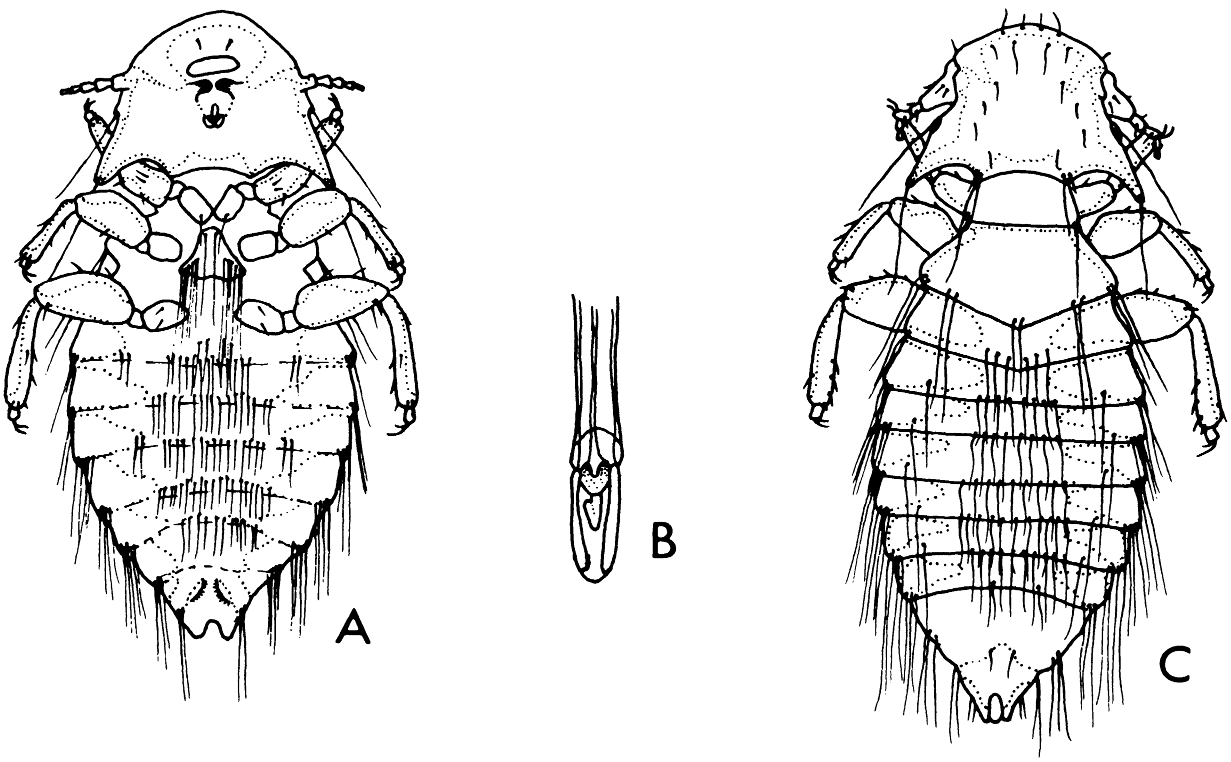


Figure 53. *Chelopistes meleagridis* (large turkey louse): ***A***, Ventral view of female; ***B***, male genitalia; ***C***, dorsal view of male. Redrawn with minor modification by Jan Read from Emerson (1962a); courtesy of Journal of Kansas Entomological Society.

41 °C temperature gradient, females placed eggs within the 39–41 °C zone. About twice as many eggs were deposited on the feather contour (see fig. 56 for identification of feather parts) as on the fluffy and silky portions combined. Only one or two eggs were placed on one feather, and they were in the silky part with the attachment end toward the skin. A temperature of 40 °C was favorable for incubation. Nymphs preferred to rest on body feathers, especially breast feathers, and almost no nymphs were counted on feathers on the tail and wing. Adult lice were more versatile; a few were found in all body regions, but the greatest numbers were found on body feathers. Both nymphs and adults were usually found in the ventral fluffy part of the feather near the rachis. Apparently, the fluffy part was the sole food of nymphs and adults.

Clayton (1991a) decided that the number of *C. bidentatus compar* on healthy birds is usually small or, at most, moderate: Averages of 400–700 lice per bird are common. But infirm pigeons, which cannot groom themselves normally, may be infested with a few thousand lice per bird. The small pigeon louse tends to remain in place after the host dies, and molted feathers often have lice and eggs still attached.

Clayton (1990b, 1991b) presented evidence that the combined infestations of *C. bidentatus compar* and *Columbicola columbae* (the two lice were not distinguished) interfered with male displays (a courtship trait) and caused female feral pigeons to choose uninfested males for mates in a significant number of his trials.

***Columbicola columbae* (slender pigeon louse)**

The genus *Columbicola* was established by Ewing (1929) for the slender species of Philopteridae found on the wing feathers of pigeons and doves (avian order Columbiformes). *Columbicola* have a long, slender head, and margins of the preantennal area are straight. The clypeus is rounded and bears two pair of spines; the front pair is flattened and the hind pair is strongly recurved. The antennae are sexually dimorphic, as the third segment of the male antenna has an appendage. The abdomen is slender, with heavily sclerotized pleural plates. Emerson (1972a) added a species to the 29 species validated by Hopkins and Clay (1952, 1953, 1955). All are parasites of columbiform birds.

Columbicola columbae (figs. 54, 55), a common parasite of domestic pigeons worldwide, is the best known of the seven North American species of *Columbicola*. It has also been reported from the Chinese turtle dove and the Formosan green pigeon of Taiwan (Martin 1934).

Female *C. columbae* deposit their eggs on the underside of the wing feathers next to the pigeon's body. Nelson and Murray (1971) found that 96.6% of eggs had been laid on the wings and only 3.4% on the head and neck. Eggs are usually attached to a feather in the spaces between feather barbs, with the attached end quite near the quill and the distal end (with its operculum) pointed toward the tip of the feather. Martin (1934) frequently found 10–20 eggs on a single feather and once counted 60 eggs on one feather. Nelson and Murray found 300 or more eggs on single wing feathers of pigeons that lacked a complete upper bill. Martin found that eggs hatched in 3–5 days (average 4.1 days) at 37 °C, but at 33 °C the incubation period was prolonged to 9–14 days. The periods of nymphal development at 37 °C were 6.73 days for first instar, 6.72 days for second instar, and 6.77 days for third instar (Rothschild and Clay 1952). Males completed nymphal development in about 2.5 fewer days than did females.

Apparently, at 74% relative humidity, 37 °C is a more favorable temperature for rearing in vitro than are the higher and lower temperatures that have been tested (Martin 1934, Conci 1952, Waterhouse 1953).

The slender pigeon louse is most often found on the wing feathers—either on the undersurface of the wing coverts or at the base of the flight feathers—but is sometimes seen on feathers on other parts of the body (Martin 1934, Ash 1960, Nelson and Murray 1971). Because of its slender shape, *C. columbae* is well adapted for living in the spaces between feather barbs (Stenram 1956); it grasps an edge of the barb with its mandibles and is thus protected from the host's preening activities.

Martin noted that nymphs were often seen on the back of the head, and Nelson and Murray found that only 37% of the nymphs they counted were on the wings. In that study, nymphs were commonly seen on the head, neck, and back feathers, but 61% of adults were on the wings. The slender pigeon louse may migrate from the wings to feed on the fluffy basal portions of the body feathers (P.R. Kettle, as cited by Marshall 1981).

Martin (1934) concluded that the sole food of *C. columbae* is the fluffy part of the feather (fig. 56), but Waterhouse (1953) noted that other feather particles and small quantities of skin scurf were seen in the crop of that louse.

In young adults, the sexes are probably about equal in number, but females survive longer than males. Nelson and Murray counted 197 males and 213 females on 3 pigeons. Copulation, as described by Martin, is similar to that reported for other Ischnocera. Eggs are deposited at the rate of one every 2–3 days. In Martin's study, two females lived 51 days, but usual female longevity was 30–40 days. Ash (1960) noted that a young crippled

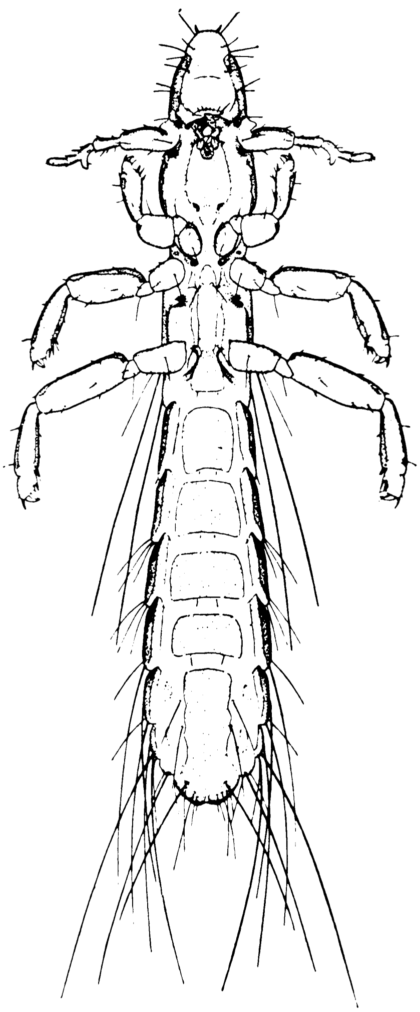


Figure 54. *Columbicola columbae* (slender pigeon louse): Ventral view of male. From Clay and Hopkins (1950), reprinted by permission of publisher. © British Museum (Natural History), 1950.

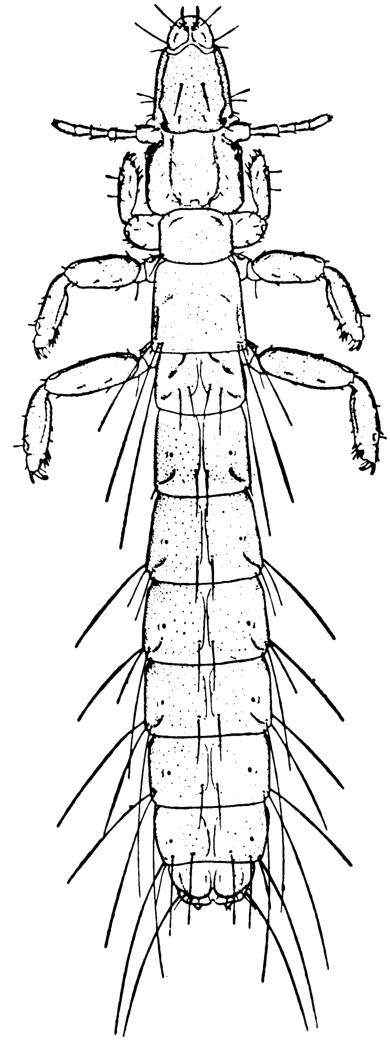


Figure 55. *Columbicola columbae*: Dorsal view of female. From Clay and Hopkins (1950), reprinted by permission of publisher. © British Museum (Natural History), 1950.

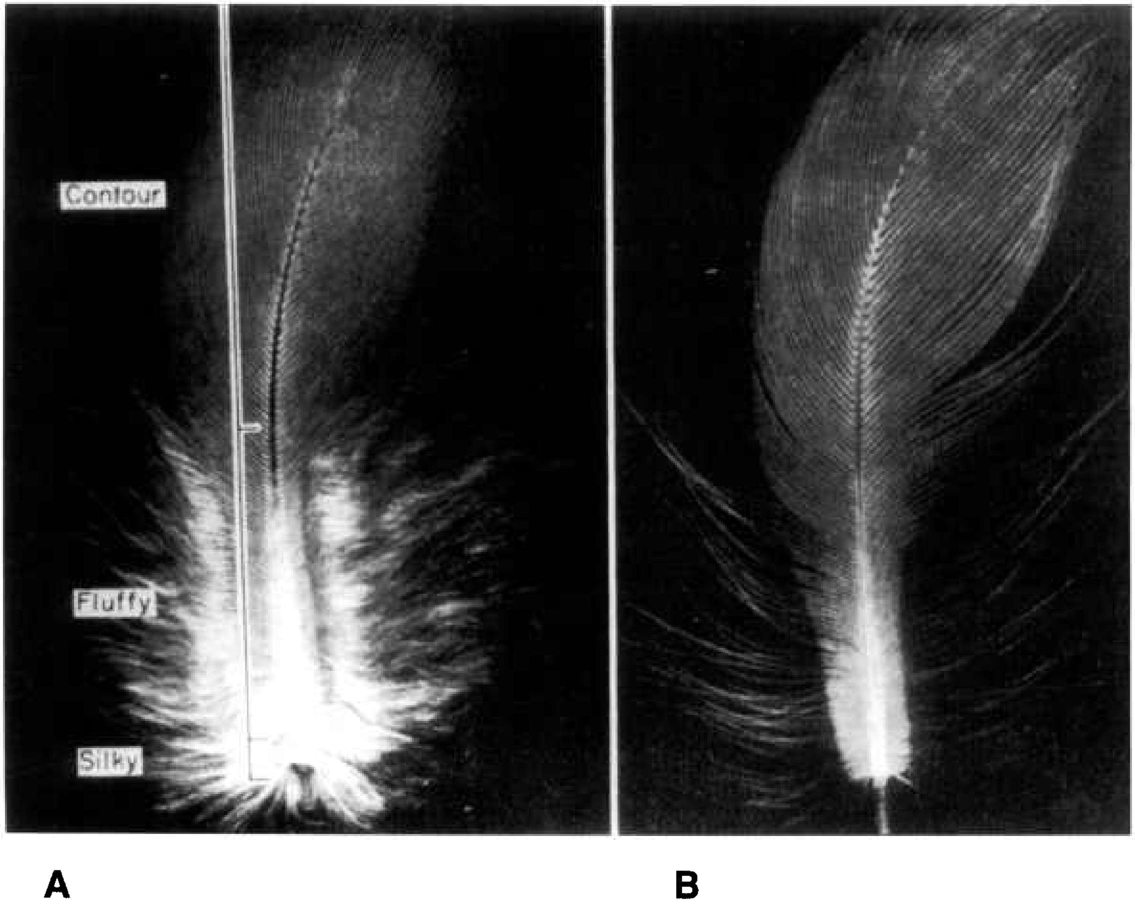


Figure 56. *A*, Undamaged body feather from pigeon with its three parts labeled; *B*, damage to a feather caused by feeding of *Columbicola columbae*. From Nelson and Murray (1971), International Journal for Parasitology, reprinted by permission of Pergamon Press Ltd, Oxford, United Kingdom.

pigeon unable to fly was infested with so many *Columbicola columbae* and *Campanulotes bidentatus compar* that, after about 6 mo, injuries by lice were probably the cause of the pigeon's death. All of the barbules and tips of the barbs of every body feather had been eaten by the lice.

FAMILY TRICHODECTIDAE

Trichodectidae was established by Burmeister (1838) when he removed *Trichodectes* [a genus in which Nitzsch (1818) had placed several species of Mallophaga from mammals] from Philopteridae, a large family of avian parasites. For many years, Trichodectidae consisted of the single genus (Kellogg 1899), but Harrison (1916) listed five genera: *Trichodectes*; *Damalinia* and *Eutrichophilus*, described by Mjöberg (1910); and *Eurytrichodectes* and *Trichophilopterus*, described by Stöbbe (1913). Ewing (1929) recognized the same five genera as valid but agreed with Mjöberg (1919), who had placed the aberrant *Trichophilopterus* from lemurs in the monotypic family Trichophilopteridae (see our remarks, p. 36). In addition, Ewing divided *Trichodectes* by describing four new genera; the type species for each was taken from *Trichodectes*. In his 1936 revision of the Trichodectidae, Ewing added to the family six of Bedford's (1929, 1932a,b) genera of primarily African Trichodectidae. Since Ewing's revision, new genera have been described by Kéler (1938), Eichler (1940), Werneck (1948), and Price and Emerson (1972). Kim et al. (1990) listed 21 genera of Trichodectidae (table 1).

The newest genus, *Thomomydoecus*, was added to the family when *Geomydoecus*, the chewing lice of pocket gophers, was divided into subgenera by Price and Emerson (1972) and then later when *Thomomydoecus* was elevated to generic rank by Hellenthal and Price (1984) (see Hellenthal and Price 1991 for a review). Hellenthal and Price (1994) have supplied a key to the 122 species and subspecies of pocket gopher lice. Hafner and Nadler (1990) and Page (1990, 1993) offered evidence that these lice and their hosts have evolved together (cospeciation) and at approximately equal rates. However, Nadler et al. (1990) hypothesized that gene flow or evolutionary change between louse populations may, in certain instances, lag behind gene flow between their hosts.

Other genera of Trichodectidae were established by elevating to generic rank a species group that was seen to have affinities to two recognized genera and was intermediate between them. Not all specialists in Mallophaga agree on the validity of some of the newer

Table 1. Genera of Trichodectidae

Genus	Hosts
Bovicola Ewing 1929	Cattle, other bovines; equines
Cebidicola Bedford 1936	Howler, spider monkeys
Damalinia Mjöberg 1910	Antelopes, deer, mostly tropical
Dasyonyx Bedford 1932	Hyraxes
Eurytrichodectes Stobbe 1913	Hyraxes
Eutrichophilus Mjöberg 1910	Porcupines
Felicola Ewing 1929	Felines
Geomydoecus Ewing 1929	Pocket gophers
Lorisicola Bedford 1936	Slow loris
Lutridia Kéler 1938	Otters
Lymeon Eichler 1943	Sloths
Neofelicola Werneck 1948	Civets, linsangs
Neotrichodectes Ewing 1929	Skunks, coatis, ringtail
Parafelicola Werneck 1948	Genets
Procavicola Bedford 1932	Hyraxes
Procaviphilus Bedford 1932	Hyraxes
Stachiella Kéler 1938	Weasels
Suricatoecus Bedford 1932	Foxes, mongooses
Thomomydoecus Price and Emerson 1972	Pocket gophers
Trichodectes Nitzsch 1810	Dogs, wolves, bears
Tricholipeurus Bedford 1929	Deer, antelopes

NOTE: Modified from Kim et al. (1990)

genera. For example, *Suricatoecus*, which shares morphological characteristics with both *Trichodectes* and *Felicola*, is currently accepted by most systematists; but *Werneckiella*, in which Eichler (1940) placed a group of *Bovicola* spp. from equines (Moreby 1978), is given (at most) subgeneric rank by Werneck (1950), Hopkins and Clay (1952), and Emerson (1972a).

The number of species of Trichodectidae worldwide was estimated to be 220 by Martin-Mateo (1977) and to be 290 by Marshall (1981). Perez-Jimenez et al. (1990), who cited Lyal (1985), placed the number of species and subspecies at 351. Emerson (1972a) listed 54 North American species. The number in South America is probably smaller, but at least 38 species are known from indigenous mammals of that continent (see appendix. A).

Trichodectidae are found worldwide, but the only Australian species are those that were introduced along with their domestic animal hosts. All the known hosts for lice in this family are mammals, but the extensive host list includes species in 19 families of 7 orders of mammals (Emerson and Price 1985). An interesting assumption by Rozsa (1993) is that *Lutridia exilis* will probably disappear from Great Britain because the population of otter hosts (*Lutra lutra*) is too low to maintain continued existence of the trichodectid louse.

Trichodectidae are distinguished from other Ischnocera by having a single, usually prominent tarsal claw on each leg, and by having only three antennal segments (fig. 57) (except for female *Eurytrichodectes*, which have five apparent segments because the distal segment appears to be divided into three) (Ewing 1936).

Genus *Bovicola*

There are 30 known species of *Bovicola* (table 2) (Emerson and Price 1981, 1982), 10 of which were moved from the subgenus *Bovicola* and 12 from other subgenera of *Damalinia* (Hopkins and Clay 1952). The remaining eight species have been described since Hopkins and Clay published their monumental work. The host list for *Bovicola* is extensive (table 2) and includes mammals in 4 families, but 20 of the louse species are from bovines.

Werneck (1950) and Wiseman (1959) characterized *Bovicola* as Trichodectidae with the body elongate but less elongate than other genera (for example, *Tricholipeurus*). The head is about as wide as it is long, with the preantennal region gently rounded, without a definite notch, and generally shorter than the postantennal region. The thorax is not modified. The abdomen is only slightly pigmented in both sexes but has sclerotized areas on typical terga, sterna, and pleura; it is distinctly pointed in the male. Abdominal setae are short and arranged in fairly regular transverse rows. The subgenital lobe of the female is somewhat expanded. The copulatory apparatus of the male has the basal plate, free endomeres, and an area of anal chitinization possibly resulting from fusion of the parameres distally.

Bovicola bovis (cattle biting louse)

Bovicola bovis may be easily distinguished from other species of cattle lice by its small size; reddish-brown color; bluntly rounded head; chewing mouthparts; and the pattern of horizontal, pigmented stripes or bars on the dorsal surface of the abdomen (fig. 57). The adult female is 1.6–1.75 mm long and 0.35–0.55 mm wide. The female was described by Piaget in 1880 and the male by Werneck in 1941 (Matthysse 1946).

Geographic distribution. *Bovicola bovis* is cosmopolitan. It has been recorded from cattle in Europe, Great Britain, Africa, Asia, and Australia as well as in North, South, and Central America. Van Volkenberg (1936) stated that the cattle biting louse is not as abundant on cattle in Puerto Rico as it is on cattle in the continental United States. Zimmerman (1944) reported a heavy infestation from an infirm cow in Hawaii (Molokai), but Alicata (1964) stated that this species is found only occasionally on cattle in that state. It is presumed that a tropical climate is unfavorable (Matthysse 1946), because populations of *B. bovis* are less numerous in tropical than in temperate regions of the world. Perhaps an abundance of sunlight, high temperatures, more moisture, or combinations of these climatic factors are responsible. However, the effects of climate on cattle lice may also be indirect, because it may be that changes in the host's physiology and hair coat are the actual causes of reductions in number or complete disappearance of lice.

The cattle biting louse is generally distributed throughout the contiguous United States and Canada, but its relative abundance compared to that of sucking lice of cattle varies by regions (Haufe 1962). In the northeastern United States, *B. bovis* often predominates (Scharff 1962); Geden et al. (1990) found that in New York in 1987, the cattle biting louse outnumbered the three species of sucking lice by 9 to 1. But in other regions of the United States, the cattle biting louse has usually been found to be less abundant than one or more of the species of sucking lice (Scharff 1962). In Orange Free State, South Africa, Fourie and Horak (1990) found more *B. bovis* on cattle than *Linognathus vituli*, a sucking louse.

Life history, habits, and ecology. In one of the earliest studies of the life cycle of *Bovicola bovis*, Lamson

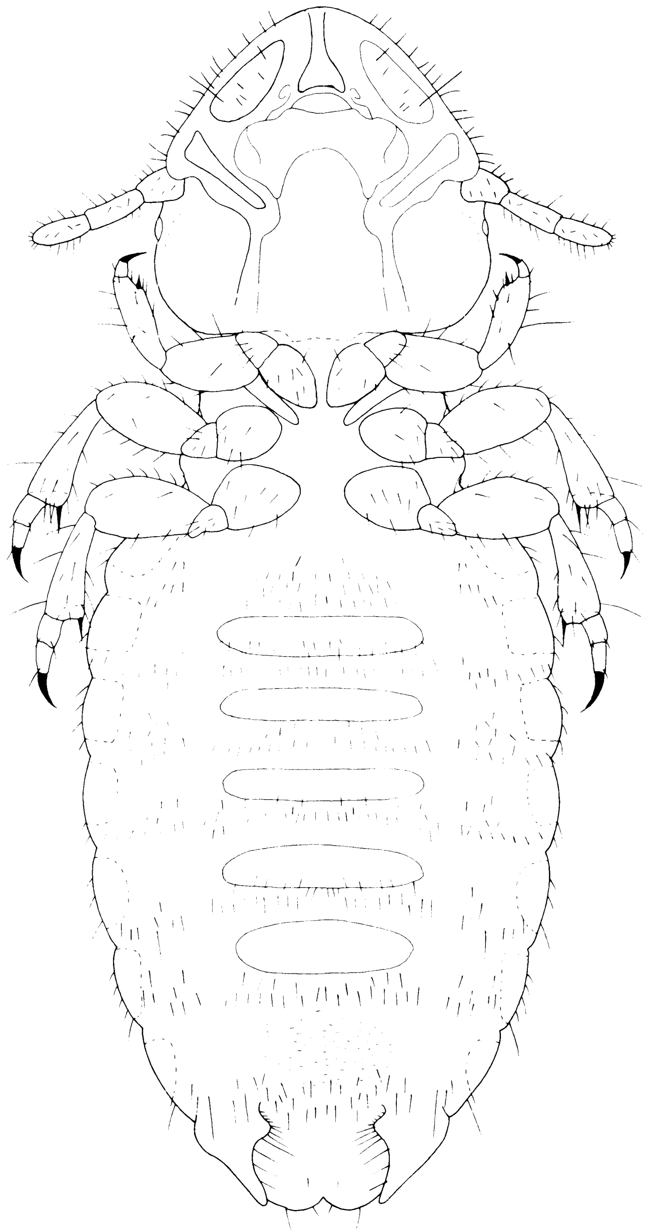


Figure 57. *Bovicola bovis* (cattle biting louse): Ventral view of female. From Emerson and Price (1975), reprinted by permission of Brigham Young University Science Bulletin, Biological Series.

Table 2. Species of *Bovicola*

Species	Host	Host family	Reference [a] page no.
adenota	Kob, puku	Bovidae	60
alpinus	Chamois	Bovidae	62
aspilopyga	East African zebra	Equidae	57
bovis	Domestic cattle	Bovidae	59
breviceps	Llama, guanaco, alpaca	Camelidae	58
caprae	Goats	Bovidae	62
concavifrons	Elk	Cervidae	58
connectens	Klipspringer	Bovidae	61
crassipes	Angora goat	Bovidae	62
dimorpha	Goral or goat antelope	Bovidae	62
equi	Domestic, wild horses	Equidae	57
fulva	Aoudad	Bovidae	62
hemitragi	Himalayan tahr	Bovidae	62
hilli	Waterbuck	Bovidae	60
jellisoni	Bighorn sheep	Bovidae	62
limbatus	Goats	Bovidae	62
longicornis	American elk, red deer	Cervidae	58
multispinosa	Bharal	Bovidae	62
neglectus	Aoudad	Bovidae	62
ocellata	Grant's zebra, donkey	Equidae	57
oreamnidis	Rocky Mountain goat	Bovidae	62
orientalis	Formosan serow	Bovidae	b
ovis	Domestic sheep	Bovidae	62
pelea	Rhebok	Bovidae	60
sedecimdecembrii	Bison, wisent	Bovidae	59
tarandi	Reindeer (caribou)	Cervidae	59
thompsoni	Serow	Bovidae	62
tibialis	Fallow deer, mule deer	Cervidae	58
zebrae	Hartmann's mountain zebra	Equidae	57
zuluensis	Chapman's zebra	Equidae	57

[a] Source: Emerson and Price (1981)

[b] Described by Emerson and Price 1982

(1918) counted the eggs deposited by isolated female lice while they were on a calf and recorded the incubation periods. Some of the progeny were transferred to another bovine host in order to observe nymphal molts and the developmental times for each instar. Shull (1932) used similar methods of determining the incubation period. Craufurd-Benson (1941) also studied the life cycle on the host and was able to isolate both single females and pairs of lice by placing them in aluminum cells that he cemented to the animal's skin.

Matthysse (1944, 1946) appears to have been the first to rear *B. bovis* in vitro. He placed lice on cattle hair in small stender dishes, added small amounts of brewer's yeast, and held groups of lice at a series of constant temperatures and relative humidities. The results of the in vitro studies were confirmed by observing smaller numbers of lice that were isolated on a young calf. Matthysse's data obtained on and off the natural host agree quite well with those of the other three workers; the data are summarized in table 3, which is somewhat modified from Matthysse (1946).

The eggs (fig. 58) are about 0.64 mm long, ovoid, flattened on one side, and translucent but almost white when first deposited. They are attached to a hair at a point near the host's skin. Although the cattle chewing louse is more motile than the sucking lice of cattle, it is not uncommon to find two or more eggs attached to the same hair.

The eggs of *B. bovis* are easily distinguished from those of other cattle lice by their smaller size and their transparent shells (Craufurd-Benson 1941). An operculum at the anterior end of the egg is pushed open by the emerging nymph, and the opened cap usually remains attached to the empty eggshell. Lamson (1918) reported an incubation period of 5–7 days, a period about 2 days shorter than that observed by other workers, but apparently he did not record the temperatures at which he conducted his studies. Hopkins and Chamberlain (1972c) found that at 37 °C and 70% relative humidity the average incubation period is 7 days.

Other life history data obtained by various workers are in good general agreement and are similar to those in table 3. Matthysse (1946) concluded that the optimum temperature for survival and growth of *B. bovis* is 35 °C and that at this temperature, the life cycle is completed in about 29–30 days. Hopkins and Chamberlain recorded a period of 25–26 days for the same cycle. Chalmers and Charleston (1980) reported 27–32 days at 35 °C. Although the skin temperature of cattle varies with changes in air temperature, solar radiation, and other external factors, it rarely varies much from the animal's body temperature if the latter is measured underneath the hair coat. Craufurd-Benson (1941) stated that skin temperatures of cattle in Great Britain seldom drop below 31 °C and usually fluctuate between 33° and 36 °C. Matthysse (1946) reported larger fluctuations in cattle skin temperatures in New York and suggested that elevated skin temperature is one of the causes of the declines in louse numbers that occur in spring and summer. His data indicate that the number of *B. bovis* on cattle declines if the host's skin temperature either exceeds 37.8 °C (100 °F) or drops below 32.2 °C (90°F). Mock and Matthysse (1977) recorded fluctuations in the temperature from 26 to 33 °C and between 27% and 40% relative humidity measured within the hair coat 2 mm from the skin when the ambient temperature was 14 °C and relative humidity was 27%.

Bovicola bovis feeds on skin scales and scurf that accumulate in the hair coat of cattle. A drawing of the alimentary canal (fig. 59) is taken from Marshall (1981).

Although small numbers of males are sometimes seen and sexual reproduction sometimes occurs, it is believed that *B. bovis* more commonly reproduces parthenogenetically. Unfertilized females isolated from males deposit viable eggs, which hatch normally. Nymphs that hatch from those eggs develop normally. Matthysse (1946) reared females for two generations in the complete absence of males. Several workers examined infested cattle and found that the percentage of males present at any one time varied from 0 to 10 and was higher only rarely (Craufurd-Benson 1941, Matthysse 1946, Hopkins and Chamberlain 1972c).

Matthysse decided that the male:female ratio varies with the density of the population; he could not find male lice on heavily infested cattle but found as many as 10% males on lightly infested hosts. He speculated that sexual reproduction may be important when populations are increasing after lice have been stressed.

To obtain information about the survival of *B. bovis* off its host, Heath (1973) determined the median length of life for unfed females held at all combinations of three constant temperatures and 10%, 50%, or 90% relative humidity. In Heath's tests, humidity did not influence survival, but adults did live longer at lower temperatures: 59 hr at 25 °C, 50 hr at 30 °C, and 42 hr at 35 °C. Nymphs survived 4–6 days at all three temperatures, but eggs did not hatch when held at 25 °C or at 90% relative humidity. At 35 °C and 10% relative humidity—the most favorable combination for incubation—the eggs hatched in 11 days. Heath concluded that if pens and stables in which lousy cattle had been quartered were vacated for 14 days, those facilities would then be louse-free.

Matthysse (1946) estimated that in the laboratory, *B. bovis* females lay one egg every 1.5 days. From this observation, the maximum number of eggs per female

Table 3. Influence of relative humidity on time required for completion of each stage of development of *Bovicola bovis* held at constant 35 °C

Stage	No. of days (range, with average in parentheses) at indicated relative humidity			
	91%	84%	75%	60%
Egg	7–10.4 (8.2)	6.1–8.9 (7.6)	5.7–9.3 (7.8)	6.6–9.3 (7.8)
1st instar	8.9–13.5 (10.0)	5.2–9.7 (7.2)	5.0–10.3 (6.8)	4.2–7.7 (5.8)
2d instar	6.0–10.6 (8.7)	4.8–9.4 (6.8)	3.8–10.5 (5.2)	3.3–6.2 (5.3)
3d instar	—[a] (12.5)	6.0–14.3 (8.5)	4.1–8.8 (5.8)	5.2–6.9 (5.9)
Preoviposition period	—	4.8–8.5 (6.7)	2.7–4.0 (3.5)	2.9–3.8 (3.4)
Life cycle, egg to adult	— (38.6)	27.3–37 (30.4)	23.1–32.1 (26.1)	22–26.6 (24.3)
Adult longevity (maximum no. days)	32	27	42	20
	Oviposition data			
Interval between eggs (no. days)	2	1.5	1.5	2
Percent hatch	10	93	59	69

[a] — = no data

Source: Data from Matthysse (1946), modified

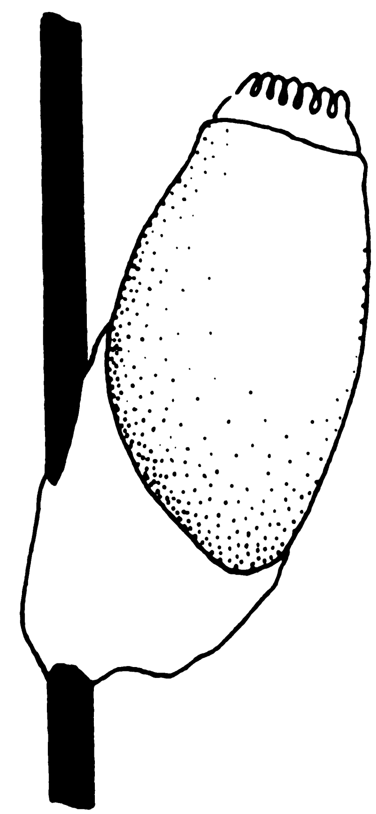


Figure 58. Egg of *Bovicola bovis* with droplet of cement used by female to attach egg to a hair. From Marshall (1981), The Ecology of Ectoparasitic Insects, reprinted by permission of Academic Press Ltd, London.

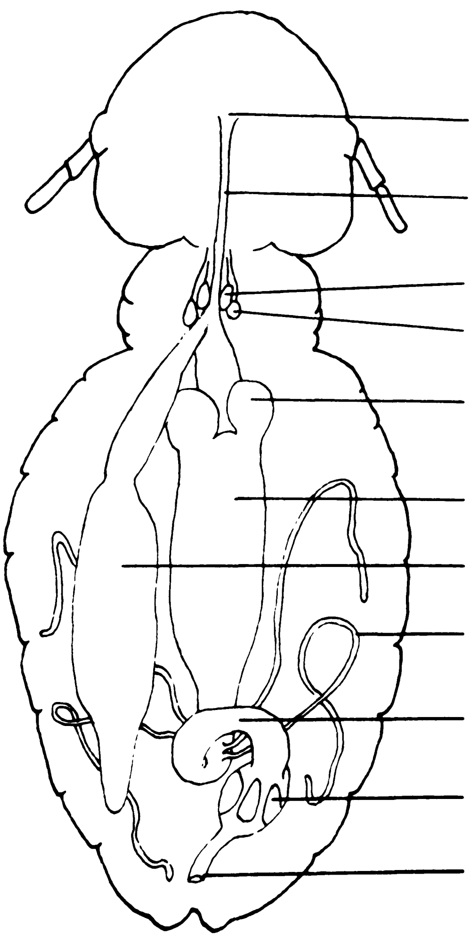


Figure 59. Alimentary canal of *Bovicola bovis.* From Marshall (1981), The Ecology of Ectoparasitic Insects, reprinted by permission of Academic Press Ltd, London.

can be calculated to be 30, but the average probably does not exceed 20. Hopkins and Chamberlain (1972c) noted that one of their laboratory colonies increased in number approximately 200-fold in 24 mo. It is quite likely that fecundity in nature exceeds that observed in laboratory colonies.

Host-parasite relationships and economic importance. Cattle are the normal hosts for *Bovicola bovis*. Collections of this louse from other hosts (the specimens are often termed "stragglers") such as cats and dogs probably occur only when unsuitable hosts have been accidentally and briefly infested with *B. bovis* (Werneck 1950). Like other Mallophaga of domestic animals, the cattle biting louse is, for all practical purposes, restricted to one host: in this case, bovine animals. This louse parasitizes Zebu cattle, *Bos indicus*, as well as various breeds of *Bos taurus* (Ansari 1951). Babcock and Cushing (1942a) mentioned the buffalo, presumably the American bison, as a host for cattle lice but did not indicate which louse species was implicated. It appears probable that a chewing louse on American bison would be *Bovicola sedecimdecembrii* (Emerson and Price 1981).

It has been frequently stated that certain breeds of cattle (for example, dairy breeds such as Holstein) are more susceptible to biting louse infestation than are other breeds (Lamson 1918, Shull 1932, Roberts 1952, Gojmerac et al. 1959, Scharff 1962). But this view has been either partially or entirely refuted by others (Babcock and Cushing 1942a, Matthysse 1946, Hoffman 1954b).

It may be true that more *B. bovis* are seen on some dairy breeds than on beef cattle, but larger numbers are likely due to holding conditions and rations commonly provided to dairy cattle and are not caused by a greater inherent susceptibility. Matthysse (1946) suggested that observers may be misled by the ease of seeing lice on the large areas of white skin on Holsteins.

That certain individual animals are highly susceptible to louse infestation is well known, but individual susceptibility to louse infestation is not limited to a particular breed. Referring to all breeds, Smith and Roberts (1956) stated that calves, yearlings, and old, undernourished cattle are the most heavily infested.

Like other species of cattle lice, *Bovicola bovis* tends to localize in a particular body area. It often congregates on the crest and side of the neck and on the shoulders, with lesser numbers on the back, rump, and tailhead (Roberts 1938b, Craufurd-Benson 1941, DeVaney et al. 1988) (fig. 60). When *B. bovis* is abundant in winter, it is rarely seen on the sides, thighs, and belly of cattle, but it may be seen in those areas later in the year as lice move to the body regions where they spend the summer.

It is well known that the cattle biting louse is most abundant during winter and early spring and that the number on cattle ordinarily declines in summer. For example, Callcott and French (1988) used a household vacuum cleaner to collect louse samples from cattle at sales barns in southeastern Georgia at regular time intervals and found that the maximum percentage of infested cattle was 24% on March 18. In a survey carried out by Geden et al. (1990) in New York, it was learned that mature cattle carry the most lice in January–March and calves in January–June.

The reasons for these seasonal fluctuations in numbers are poorly understood, but researchers have proposed some plausible explanations. Lamson (1918) and Shull (1932) noted that cattle that are not in good physical condition at any time of the year are more likely to be heavily louse infested than others and that their skin is drier because the secretion of oils is reduced. Animals with dry skin often have large amounts of scurf in the hair; Roberts (1938b) and Craufurd-Benson (1941) associated scurfiness with louse infestation. Lice are lost in spring when the winter hair coat with its scurf is shed and air temperatures increase.

Of the spring and summer climatic factors that might be detrimental to cattle lice, Craufurd-Benson (1941) considered the intrinsic effects of solar radiation as probably the most important. But this view was rejected by Matthysse (1946) and Lancaster (1957), who considered the elevated skin temperatures (41 °C, recorded on cattle exposed to full sunlight) to be harmful.

Matthysse had observed that laboratory colonies of *B. bovis* did not survive temperatures of 38 °C and higher. However, Lancaster also noted that a calf held at a constant 13 °C lost its louse infestation during summer just as fast as a similar calf that was outdoors. Jensen and Roberts (1966) found that although the skin temperature of a heifer (measured along the back) rose to a maximum of 45 °C in full sunlight in an air temperature of 33 °C, the skin temperatures of louse microhabitats on the animal's side ranged from 37 to 39 °C.

Pastures improve in spring at the same time that *B. bovis* populations decline. This fact has suggested that improved host nutrition inhibits louse reproduction and survival through its influence on the shedding of winter hair with its scurf and debris and on the increased oiliness of the new, short hair (Shull 1932, Roberts 1938a,b). In a study carried out in Idaho, Shull found that the oil content of the hair was 1.885% for Holsteins and 6.310% for Jerseys; in all animals examined, Holsteins had more lice than Jerseys. Utech et al. (1969) noted that a group of cattle in their study with "long,

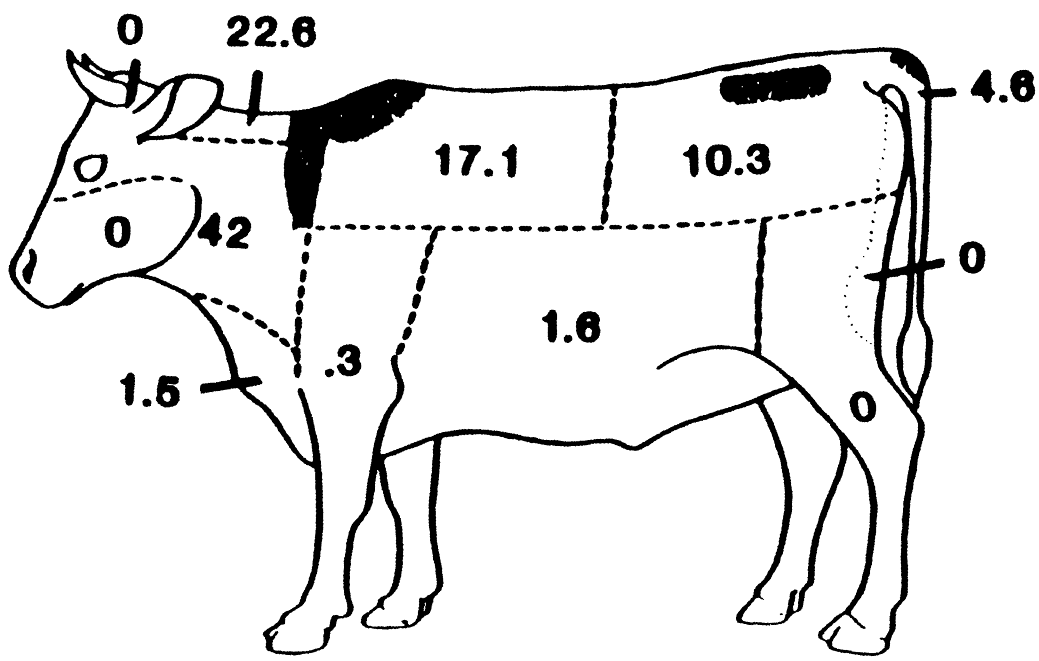


Figure 60. Average numbers of *Bovicola bovis* counted on different parts of a cow's body. From DeVaney et al. (1988), reprinted by permission of Southwestern Entomologist.

harsh and scurfy" hair coats had 43 times more *B. bovis* than did another group with "sleek, glossy coats." Calves in Nebraska on a high nutrition level had fewer lice and were affected less by them than were calves that received only a maintenance ration (Ely and Harvey 1969). Melancon (1993) agreed that animals on a high plane of nutrition are less likely to be infested by lice. However, because *B. bovis* infestation of the test cattle of Gojmerac et al. (1959) increased in winter and declined in spring even though the ration had not changed, they concluded that diet was not a factor in susceptibility to louse infestation. But they had not compared well-fed cattle with undernourished cattle.

Gojmerac et al. (1959) failed to find a positive correlation between the quantity of ether-alcohol-soluble skin secretions and louse counts on dairy heifers. Although the quantity of secretions recovered from the skin was low during winter, the number of lice declined (in late February to mid-March) before skin secretions increased significantly (in April). Also, as a rule, the number of lice begin to decline in late winter before pastures improve. Yeates (1955, 1958) did not find a difference in the quantity of ether-extractable oils recovered from the hair of Shorthorn heifers with dry hair and the quantity from heifers with sleek hair. But Yeates did find that normal, springtime shedding of the winter hair coat was delayed indefinitely in undernourished cattle.

But it may be that the influence of climatic factors, host nutrition, breed, and other factors on louse populations has been overemphasized. Lewis and Christenson (1962) and Lewis et al. (1967) in Oregon demonstrated that populations of *B. bovis* (and a sucking louse, *Linognathus vituli*) increased rather than decreased during late spring and early summer if host cattle were restrained from licking themselves by holding them in a rigid stanchion. Counts of *B. bovis* as high as 16/cm^2 over the entire upper body were recorded throughout June and July; but after the cattle were released from stanchions, they licked off almost all lice within 3 days. Mock (1974) demonstrated that if cattle were held indoors and prevented from licking, *B. bovis* would increase to 20 adults/cm^2 overall and to 80 adults and hundreds of nymphs/cm^2 in favored spots. Utech et al. (1969) suggested that reduced self-grooming by cattle given only a subsistence ration was one of the reasons for their heavy infestation with *B. bovis* in late spring.

An anomaly of the host-parasite relationship between lice and cattle is the rare highly susceptible animal that remains heavily infested the year round—an animal often labeled "carrier" by livestock producers. Carriers occur in both sexes and in many breeds, and typically they never develop resistance to lice. Their existence is often discussed, but exact reasons for their extreme susceptibility remain a mystery. Snipes (1948) separated 100 carrier cattle from a herd of over 3,000 in Montana for one of his louse control tests. Mock (1987) pointed out that the number of carriers seldom exceeds 1%–2% of the herd. Bulls are carriers in a disproportionate number of instances. This may be because bulls are often housed, because their hair is longer and more dense, and because the bull's massive neck and shoulders make it harder for the animal to groom itself. Also, older cows in poor physical condition are more apt to be carriers.

Transfer of the cattle biting louse from one host to another is believed to take place usually while cattle are in direct contact with each other, but Bay (1977) reported occasionally seeing louse nymphs and adults attached to horn flies that he collected from cattle. Phoresy was suggested, but it is very difficult to assess the importance of this means of louse dissemination.

Like other Mallophaga, *B. bovis* does not pierce the skin of its host but instead uses its chewing mouthparts to feed on skin particles, fragments of hair, and other skin debris that it encounters in its microhabitat. (The alimentary canal of the cattle biting louse is illustrated in fig. 59.) Nevertheless, when present in considerable numbers, cattle biting lice annoy and irritate their host and cause the animal to rub, lick, scratch, and bite itself to the extent that patches of skin become raw and encrusted; often the hair is lost from areas 2–10 cm in diameter or even larger. The lice sometimes congregate underneath a loose scab and can be seen between it and the raw skin. When cattle rub in an attempt to relieve the itching caused by lice, they damage and eventually destroy fences, gates, hayracks, barns, and other barnyard structures. Loss of hair and patches of skin caused by rubbing and scratching may damage the animal's heat-regulation mechanism (DeVaney et al. 1988).

It is generally accepted that a single chewing louse is less injurious than a single sucking louse, but because *B. bovis* may occur in much larger numbers than sucking lice, it is in some regions the most injurious species of cattle lice. Matthysse (1946) considered *B. bovis* the economically most important species in New York State. Farther west the situation apparently changes; *B. bovis* is less abundant than the three species of sucking lice in Montana and is less injurious there and in other western states (Scharff 1962). However, the relative abundance of the species may vary from year to year: In a 3-yr study in western Nebraska, infestations of *B. bovis* were more severe than those of sucking lice during the first year of the study, but less severe the other 2 yr (Gibney et al. 1985).

Lice retard the growth of young beef and dairy cattle, and heavily infested dairy cows produce less milk than do uninfested cows. Severe louse infestation may be a contributing factor to winter death losses of cattle that lack proper care. Cattle, particularly calves, sometimes respond to louse infestation by increasing the time spent in licking; as a result, hair balls may form in the gut (Lehane 1991).

In New York State, dairy heifers suffered more injuries than did other classes of cattle, in part because they often receive less owner attention (Matthysse 1946). But it has been noted that calves that were housed outdoors in individual hutches and without physical contact with other cattle had only half as many lice as calves that spent the winter in barns as part of a herd (Geden et al. 1990).

Haufe (1962) stated that in Alberta, heavily infested calves often fail to achieve normal weight gains. Weight gains were reduced by as much as 0.21 lb/day by calves in Nebraska that were infested with *B. bovis* and other lice (Campbell 1992a). On the other hand, Scharff (1962) concluded that lice are a relatively minor problem in Montana cattle, primarily because only 1%–2% of the animals are infested by enough lice to injure them. Also, Kettle (1974) in New Zealand and Oormazdi and Baker (1980) in Ireland found that moderate numbers of *B. bovis* did not interfere with weight gains. But louse infestation did harm general appearance and therefore reduced the market value of cattle. Animals that rubbed vigorously injured their hides and lowered the value of processed hides (Oormazdi and Baker 1980).

In summary, when cattle are infested with so many *B. bovis* that obvious skin irritation and vigorous self-grooming occur, economic losses result if no attempt is made to control the lice. Stocker cattle and calves alone may suffer losses from lice infestation of $38 million (Kunz et al. 1991) even though only 10% of stockers and calves in the northern states can be expected to carry heavy louse infestations. Kunz (1994) stated that losses of 0.02 kg/head in the average daily gain of infested feeder cattle have been reported, but well-nourished cattle with light to moderate louse infestations suffer little or no loss. Drummond et al. (1981) estimated that the four species of cattle lice in the United States caused economic losses of $126 million per year.

Because the injuries inflicted on cattle by *B. bovis* are often obvious to their owners, many materials have been used to control this louse. They range from home remedies of the previous century to the most sophisticated of the modern insecticides. The control measures for chewing lice are usually the same as those for sucking lice, and louse control on cattle is often similar to control on other large animals. For these reasons, louse control on cattle is discussed at the end of this book (see p. 209).

Bovicola caprae (goat biting louse)

The most common louse on all classes of goats in North America seems to be *Bovicola caprae*, the goat biting louse (fig. 61) (Wiseman 1959). It has a brownish-red head and thorax. The yellowish abdomen has brown crossbands that are lighter and not quite as wide as those on *B. limbatus*, which also occurs on goats. The typical female is slightly smaller, about 1.5 mm long, and not as robust in appearance as *B. limbatus*. The males have a truncated anterior margin of the head. They are slightly larger and more robust in appearance than the males of *B. limbatus*. However, these differences between the species are variable, so these two species of goat lice can be differentiated only by examining the male genitalia.

Distribution of the goat biting louse is believed to be cosmopolitan. Werneck (1950) reported it from Georgia, South Carolina, Texas, and California. He also examined collections from Argentina, Guyana, Colombia, and many localities in Brazil, Costa Rica, and Cuba. Tagle (1966) found it in Chile. In addition, it has been recorded from France, Uganda, South Africa, India (Singh and Chhabra 1973), Australia (Roberts 1952), and New Zealand (Heath 1973). Lozoya-Saldaña et al. (1986) reported that *B. caprae* was abundant in Coahuila, Mexico.

Life history. Female *B. caprae* place their eggs on the goat's hair at a point near the skin. The incubation period is influenced by environmental factors and can be expected to vary from 7 to 14 days. Heath (1973) observed that eggs held at a constant 30 °C and at either 10% or 50% relative humidity hatched in 8–10 days. But in his laboratory, eggs held off the host at 25 and 35 °C did not hatch. Although they are quite motile, the nymphs often do not move far from the eggshells. Some nymphs may form small clusters in the body region where the eggs were deposited, but others may disperse over all the hairy parts of the body. They feed on epidermal scales and other skin debris and grow by the process of gradual metamorphosis. After three molts that are spaced 5–10 days apart, the adult louse emerges from the discarded nymphal cuticle.

The average preoviposition period is 4–6 days. Longevity of the adults may range from 10 to 43 days. In the laboratory, an entire life cycle from egg to egg required 36.7 days (Butler 1985). The rate of reproduction may be higher than that of *Bovicola bovis*; Heath (1973) calculated that females lay one egg each 24 hr.

Ordinarily the goat biting louse transfers from one host to another while goats are in close contact with each

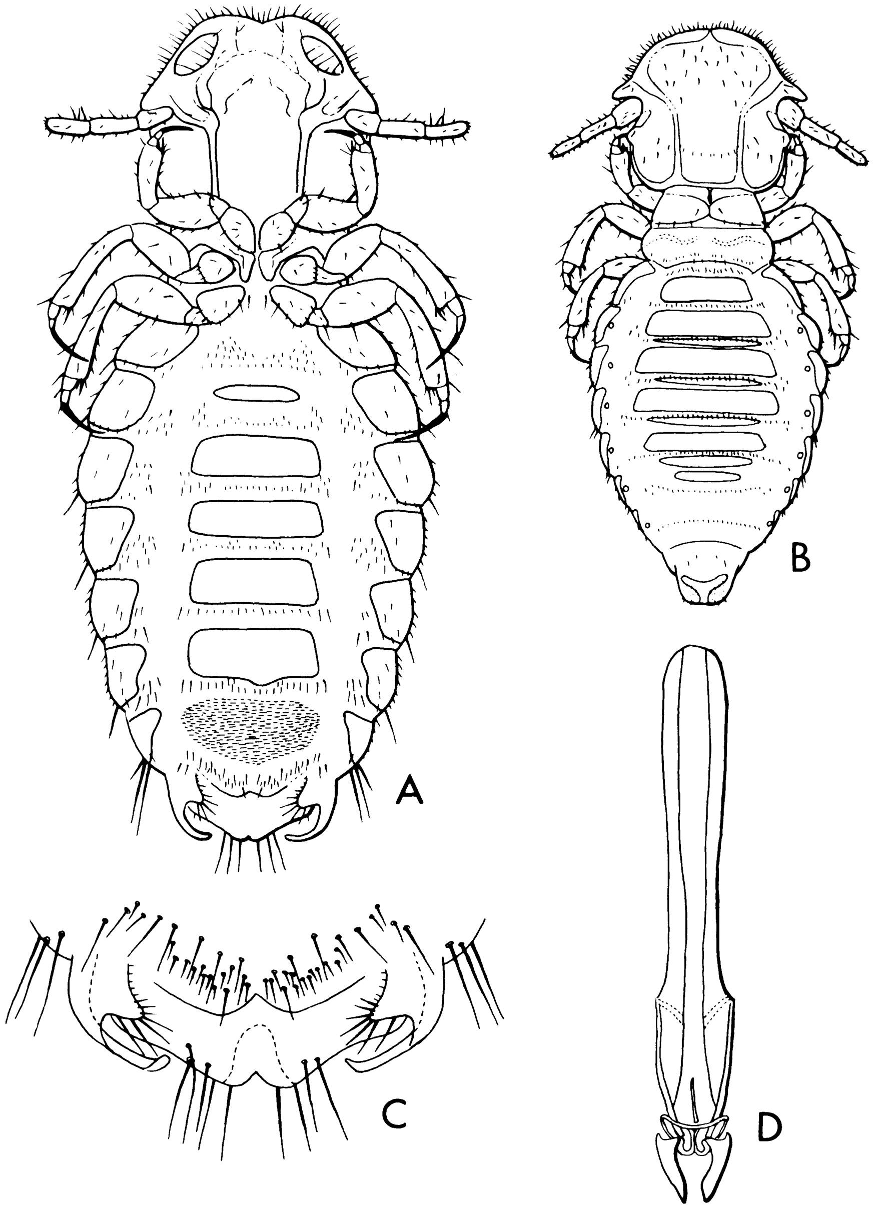


Figure 61. *Bovicola caprae* (goat biting louse): ***A***, Ventral view of female; ***B***, dorsal view of male; ***C***, female terminalia; ***D***, male genitalia. Redrawn with minor modification by Jan Read from Emerson and Price (1975); courtesy of Brigham Young University Science Bulletin, Biological Series.

other. However, since some stages of the louse can survive off the host for short periods of time, it is possible for goats to become infested by occupying pens, trucks, chutes, and other facilities that have been previously occupied by other goats. Heath (1973) found that at a constant 25 °C, adult *B. caprae* lived off the host for an average of 122 hr, much longer than at 30 or 35 °C. Nymphs survived for about the same time: 4–6 days. By adding nymphal longevity and incubation period, Heath concluded that in the absence of a host, all viable forms would perish within 14 days. His overall conclusion was similar to that of Thorold (1963), who decided that without a host, all goat biting lice would die within 15 days. However, the latter investigator reported that in his tests, newly hatched nymphs did not survive for longer than 6 hr without feeding.

Host-parasite relationships and economic importance. Apparently the primary host of *Bovicola caprae* is the short-haired goat *(Capra hircus*). It is sometimes referred to as the common or domestic goat and is best known in the southwestern United States as the Spanish goat (Price et al. 1967a). The chewing lice on Angora goats are more likely to be *Bovicola crassipes* or *B. limbatus*, while *B. caprae* is most frequently found on short-haired (Spanish) goats (Emerson 1962b). However, Thorold (1963) considered *B. caprae* to be a major pest of Angoras in South Africa. Various breeds of milch goats may also be suitable hosts. Pratap et al. (1991) observed that 36% of a flock of Black Bengal goats in India were infested with *B. caprae*. Reports of *B. caprae* from hosts other than goats have probably been based on misidentifications or the collection of stragglers. Babcock and Cushing (1942c) pointed out that sheep, dogs, and burros that are closely associated with goats may act as temporary carriers of goat lice.

Because the two species are so similar in appearance, it is probable that *B. caprae* and *B. limbatus* have been frequently confused with each other in the literature. As a result of this confusion, it is difficult to evaluate the reports of host injury caused by *B. caprae*, but it appears that the nature of the damage caused by the two species is quite similar—perhaps identical.

Goat biting lice feed on or near the surface of the skin. When numerous, they irritate and annoy the goats and cause the animals to rub and scratch. Loss of hair and a rough hair coat may result.

Bovicola caprae are more abundant in winter but even then are considered less injurious than the goat sucking louse, *Linognathus stenopsis*. The U.S. Department of Agriculture (1976) estimated that on sheep and goats together, lice as a group caused average annual losses of $8 million.

Bovicola crassipes (=*B. penicillata*)

Because it is larger, yellow, and has a hairy appearance (fig. 62), *Bovicola crassipes* is easily distinguished from the other two species of chewing lice on goats. The average lengths are 2.2 mm for females and 1.64 mm for males. Both sexes are densely covered with setae (giving a hairy appearance), the forehead is semicircular, and the antennae are attached farther forward than are the antennae of the other species (figs. 63–70). Although Stoetzel (1989) listed the Angora goat biting louse as the common name for *B. crassipes*, this name in the past was given to *Bovicola limbatus*.

Specimens from Delaware, Texas, and South Africa were examined by Werneck (1950), but the geographic distribution is assumed to correspond to that of the type host, the Angora goat. Emerson and Price (1985) stated that *B. crassipes* has not been found on short-haired goats. Although they are rare, heavily infested sheep have been reported by Hopkins (1949) and Werneck.

From the observations of Hopkins and Chamberlain (1969), who reared *B. crassipes* in vitro at 35 °C±1.5°, it appears that its life history is similar to that of other species of *Bovicola*. Eggs are deposited singly and are cemented to two or three fibers of mohair. For some reason, as many as 25% of eggs in some of the groups were damaged by punctures of the chorion, which appeared to have been made by the lice. When damaged eggs were excluded from the count, the hatch averaged 94% and survival to the adult stage averaged 65.7%. The life cycle is summarized in table 4.

The male-female ratio was 1:1.2, and females that were isolated from males did not reproduce parthenogenetically. Once oviposition began, eggs were produced at the rate of 1.16/days, but oviposition declined after females were 15 days old. These data suggest that each female produces only 12–15 eggs, but the number may be higher; Hopkins and Chamberlain observed an approximate fivefold increase in the number of adults in their colony in 2 mo. The life cycle from egg to egg averaged 36.7 days. For some reason, the development of a small percentage of the first-instar nymphs was arrested, and their molt occurred 9–53 days later than that of most of the nymphs. These whitish nymphs turned dark on the third or fourth day and became quiescent.

Because both species may be present on the same goat at the same time, it has not been possible to distinguish the damage caused by *B. crassipes* from that

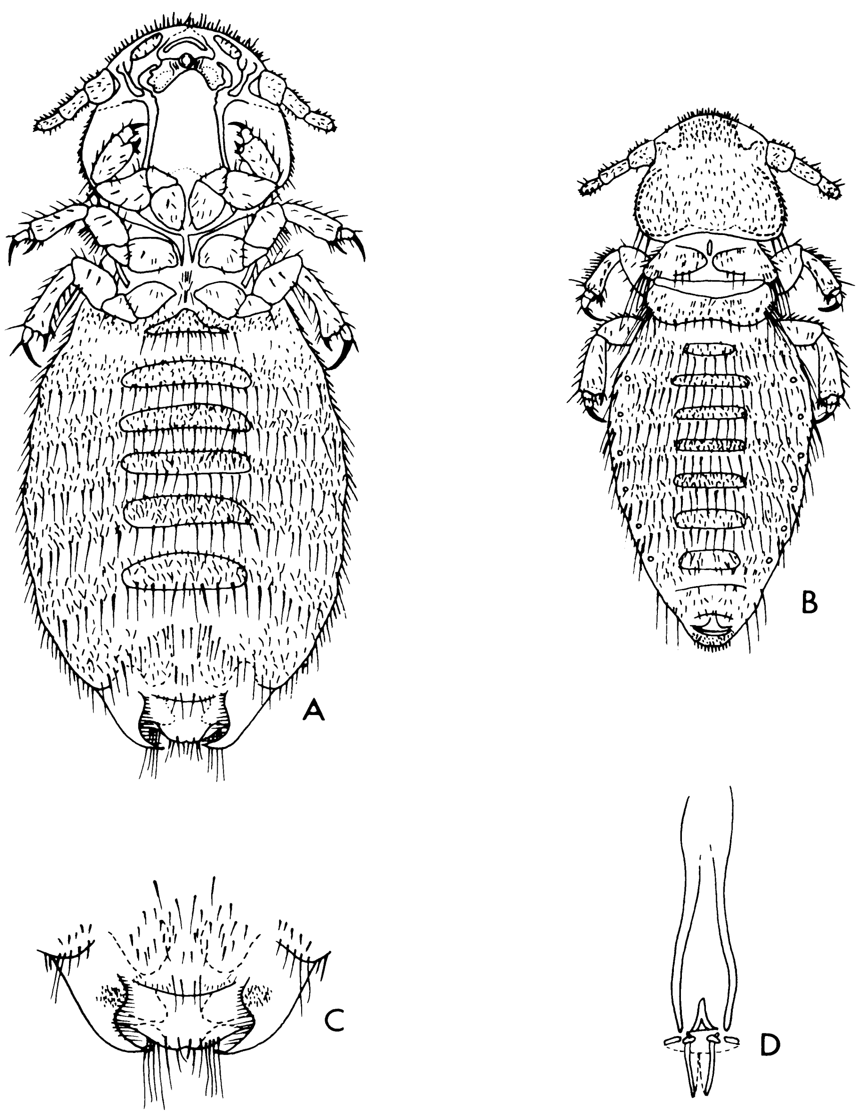


Figure 62. *Bovicola crassipes*: ***A***, Ventral view of female; ***B***, dorsal view of male; ***C***, female terminalia; ***D***, male genitalia. Redrawn with minor modification by Jan Read from Werneck (1950); courtesy of Memórias do Instituto Oswaldo Cruz, Rio de Janeiro, Brazil.

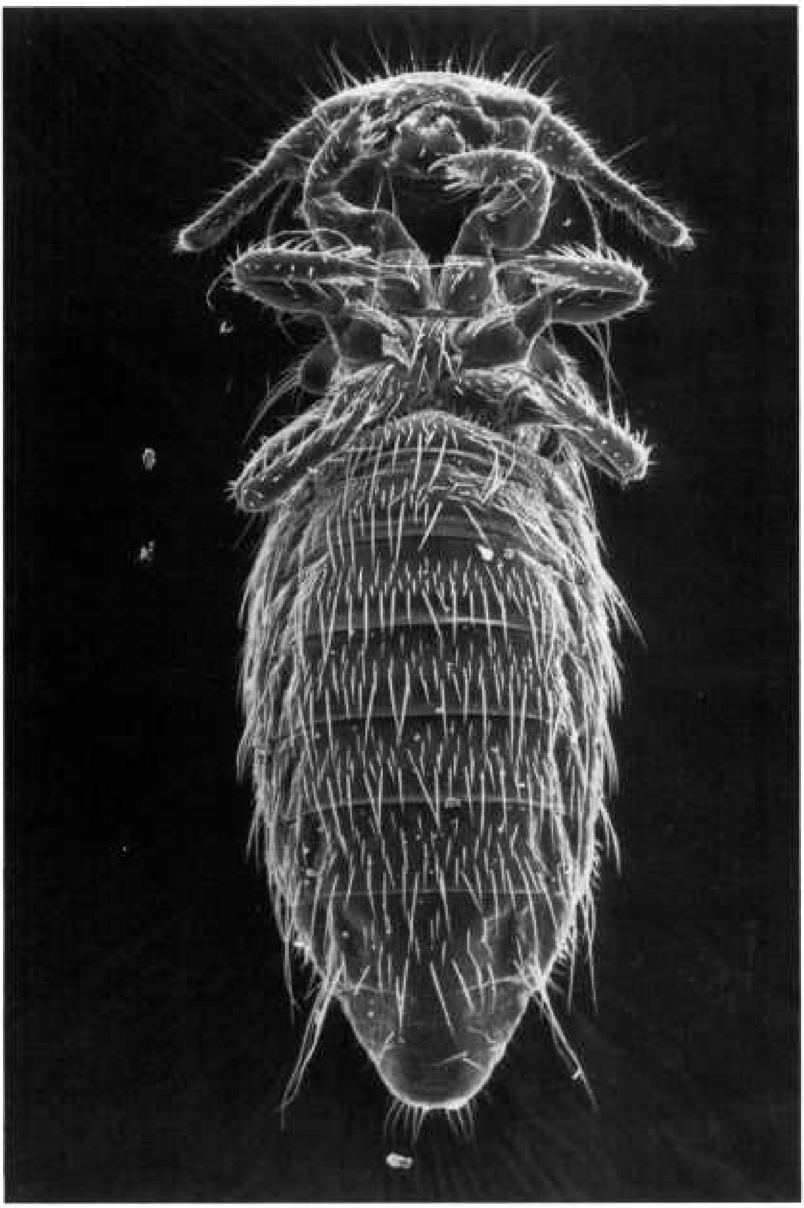


Figure 63. *Bovicola crassipes*: Ventral view of male. SEM × 50, by Theresa Droste; courtesy of Department of Entomology, Texas A&M University.

Figure 64. *Bovicola crassipes*: Ventral view of female. SEM × 33, by Theresa Droste; courtesy of Department of Entomology, Texas A&M University.

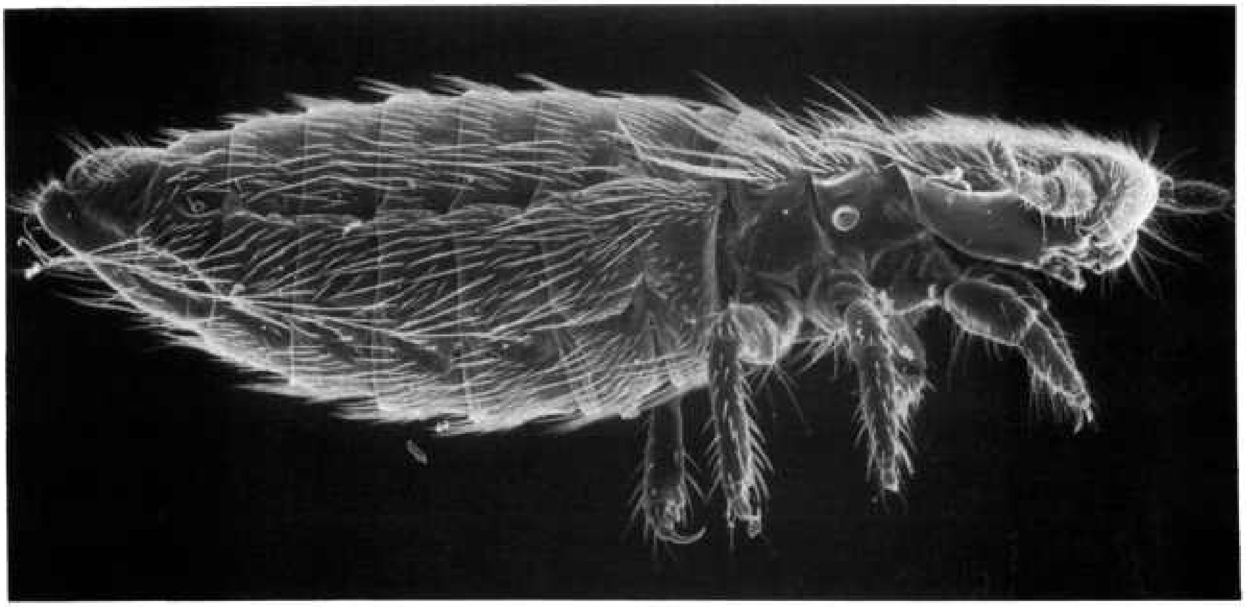


Figure 65. *Bovicola crassipes*: Side view of adult insect. SEM × 47, by Theresa Droste; courtesy of Department of Entomology, Texas A&M University.

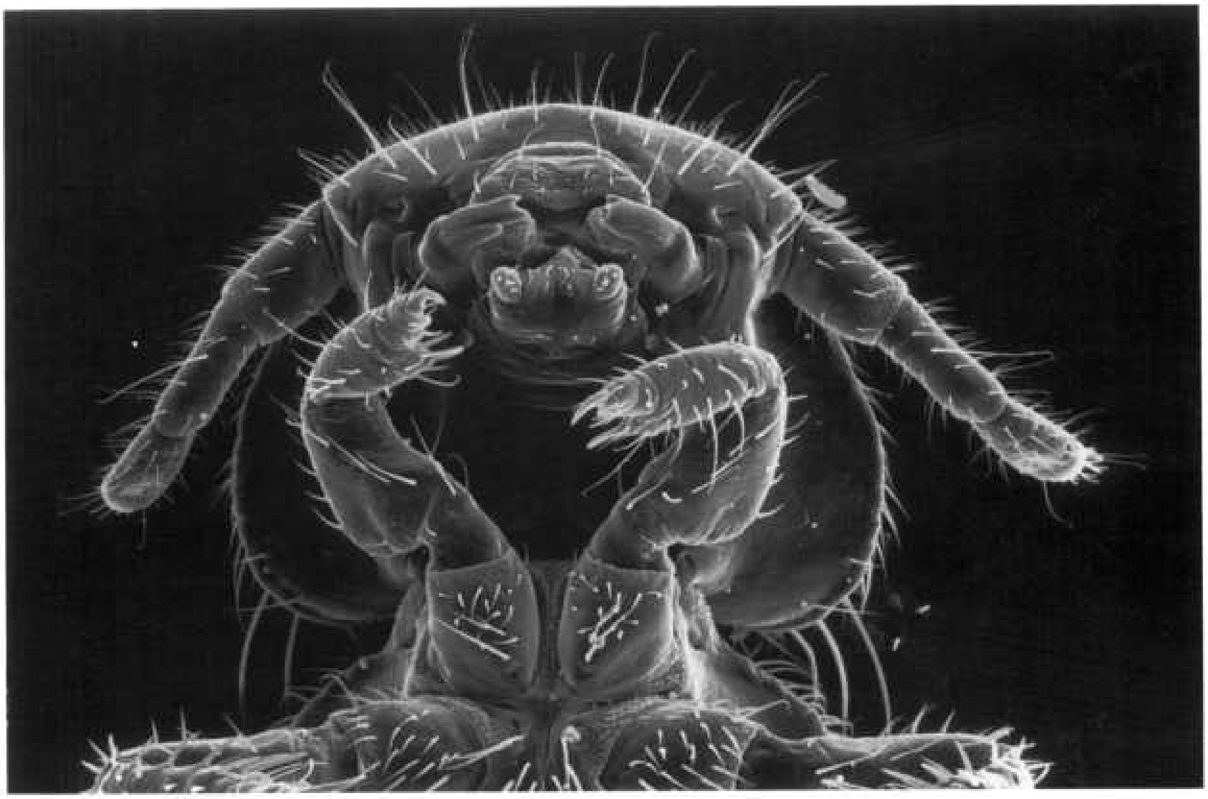


Figure 66. *Bovicola crassipes*: Underside of male head. SEM × 110, by Theresa Droste; courtesy of Department of Entomology, Texas A&M University.

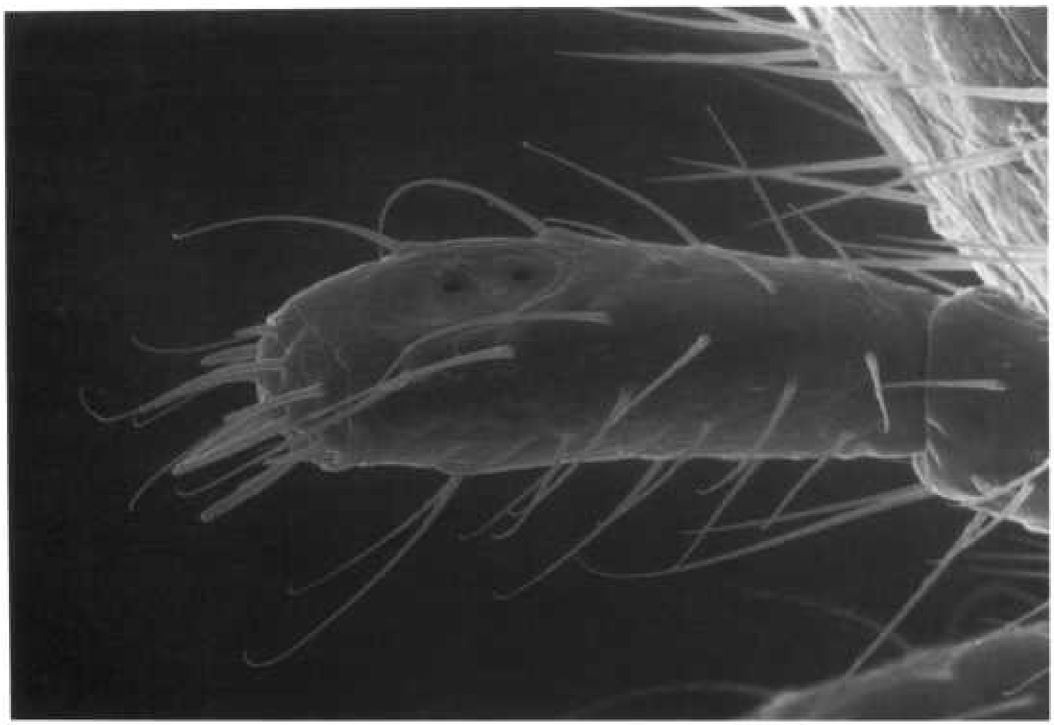


Figure 67. *Bovicola crassipes*: Terminal segment of antenna, with sensilla visible on top surface. SEM × 550, by Theresa Droste; courtesy of Department of Entomology, Texas A&M University.

Figure 68. *Bovicola crassipes*: Right front tarsus. SEM × 300, by Theresa Droste; courtesy of Department of Entomology, Texas A&M University.

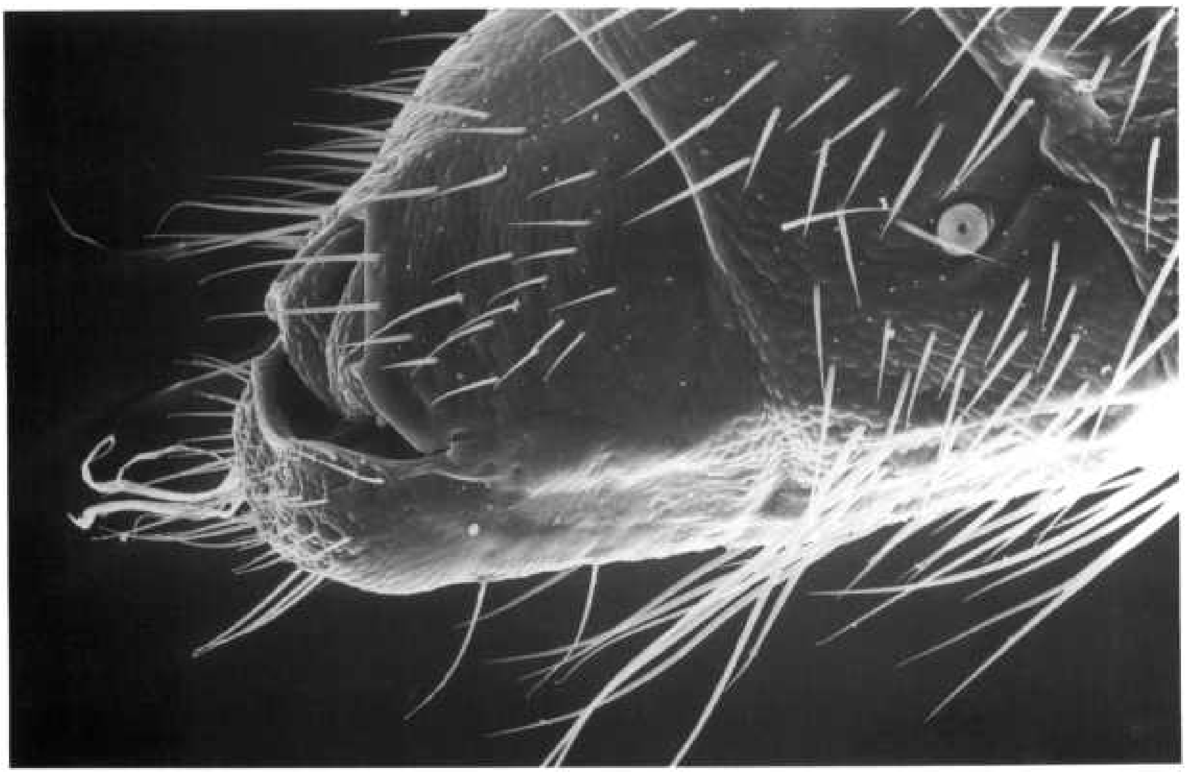


Figure 69. *Bovicola crassipes*: Tip of abdomen, tilted. SEM × 220, by Theresa Droste; courtesy of Department of Entomology, Texas A&M University.

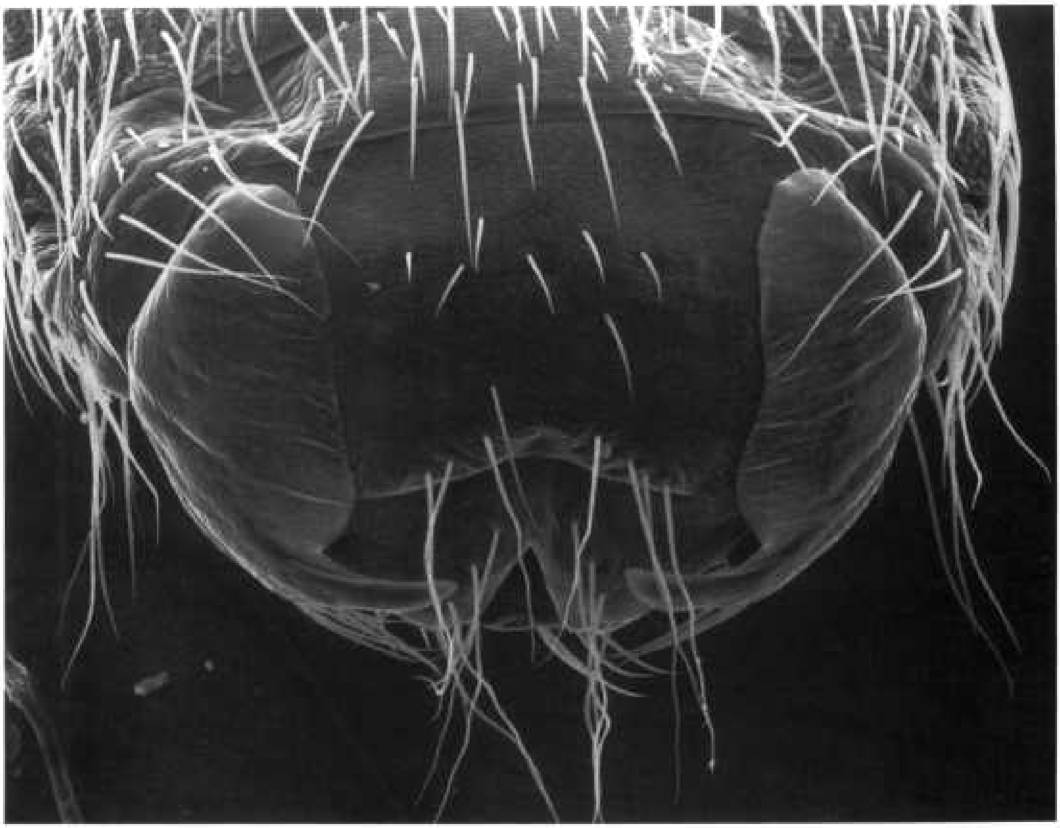


Figure 70. *Bovicola crassipes*: Dorsal view of tip of abdomen. SEM × 130, by Theresa Droste; courtesy of Department of Entomology, Texas A&M University.

Table 4. Life cycle of *Bovicola crassipes* [a]

Stage	Time (days) required for development	
	Range	Average
Egg	9–11	10.1
1st instar	6–11	7.6
2d instar	5–9	6.7
3d instar, males	6–9	7.5
3d instar, females	6–10	8.2
Preoviposition	3.5–5.5	4.1
Adult longevity, males	10–42	21.8
Adult longevity, females	8–43	19.5

[a] Reared at 35 °C±1.5° and 72% relative humidity
Modified from Hopkins and Chamberlain (1969)

caused by *B. limbatus*. However, *B. crassipes* may cause more matting of the mohair since it commonly attaches its egg to two or three strands of mohair instead of one. Price et al. (1967a) considered that biting lice as a group reduced the clip of mohair by as much as 10%–25%.

Bovicola equi (horse biting louse)

The chewing louse of horses, *Bovicola equi* (fig. 71), can be recognized by the evenly rounded anterior margin of its head, its dense covering of setae, and a small first antennal segment in males. Females are 1.6–2.16 mm long, and males 0.73–1.93 mm. The head and thorax are brown, and the yellowish abdomen has clear, short transverse bars.

The horse biting louse is worldwide in distribution. Werneck (1950) listed records from Brazil, numerous states in the United States, Africa, and the Philippines. It is also known from Australia (Calaby 1970), Great Britain, and the British West Indies (Moreby 1978).

The eggs of *B. equi* are placed on the fine hairs of the horse's coat with the attached end near the skin (Murray 1957d). Occasionally more than one egg is placed on a single hair. Apparently the coarse hairs such as those in the mane are too large for the female to use, because the eggs of *B. equi* are never found on them. In Murray's study, the number of eggs laid was strongly influenced by temperature. The optimum temperature was 35 °C, and the number of deposited eggs sharply declined when adult lice were held at temperatures lower than 32.5 °C and higher than 37.5 °C. The eggs hatch in 8–10 days (Roberts 1952).

Populations of the horse biting louse usually increase in winter and decline during the warmer months, but Butler (1985) observed that in Florida, populations may remain high throughout the year. Horses shed the fine hairs in their coat twice a year. When those hairs are lost in spring, a large percentage of louse eggs are also lost; in one observation, 80% were lost (Murray 1957d). Horses that do not shed their hair (because of poor physical condition or other reasons) are more likely to be heavily louse infested. An association between long shaggy hair and large numbers of lice has been frequently noted. Knapp (1985) estimated that 5% of pastured horses in the United States have visually detectable lice, chewing and sucking, during the winter months.

The normal host of *B. equi* is the horse. It has also been collected from donkeys (Emerson 1972a), the Mongolian wild ass, and the Mongolian wild horse (Moreby 1978). *B. equi* localizes on the sides of the neck, in the flanks, and at the base of the tail; but when horses are heavily infested, the lice may be found over most of the body except the lower legs, tail, mane, and ears.

Horses react to severe infestations of *B. equi* by rubbing against any convenient object, kicking, and stamping their feet. Patches of hair are rubbed from the neck, shoulders, and flanks, and frequently the top of the tail is rubbed bare. Animals suffering from louse infestation are likely to become nervous and irritable (Bishopp 1942). A rough, unkempt appearance can cause significant losses in the monetary value of horses.

Bovicola limbatus (Angora goat biting louse)

Because of similar appearance and frequent occurrence on the same host, *Bovicola limbatus* (fig. 72) is often misidentified as *Bovicola caprae*. Females of the two species are especially difficult to separate. The typical female of *B. limbatus* is about 1.5–2 mm long, and the males are slightly shorter. The anterior margin of the head is flattened but slightly concave at the apex (figs. 73, 74), and the antenna has two sensilla on the terminal segment (fig. 75). Brown bands are present on the abdominal segments. Males of the two species are more easily separated because the parameres of *B. caprae* are thicker and more recurved than those of *B. limbatus* (R.D. Price, personal communication, 1995).

Distribution of the Angora goat biting louse is worldwide and coincides with that of its host. Werneck

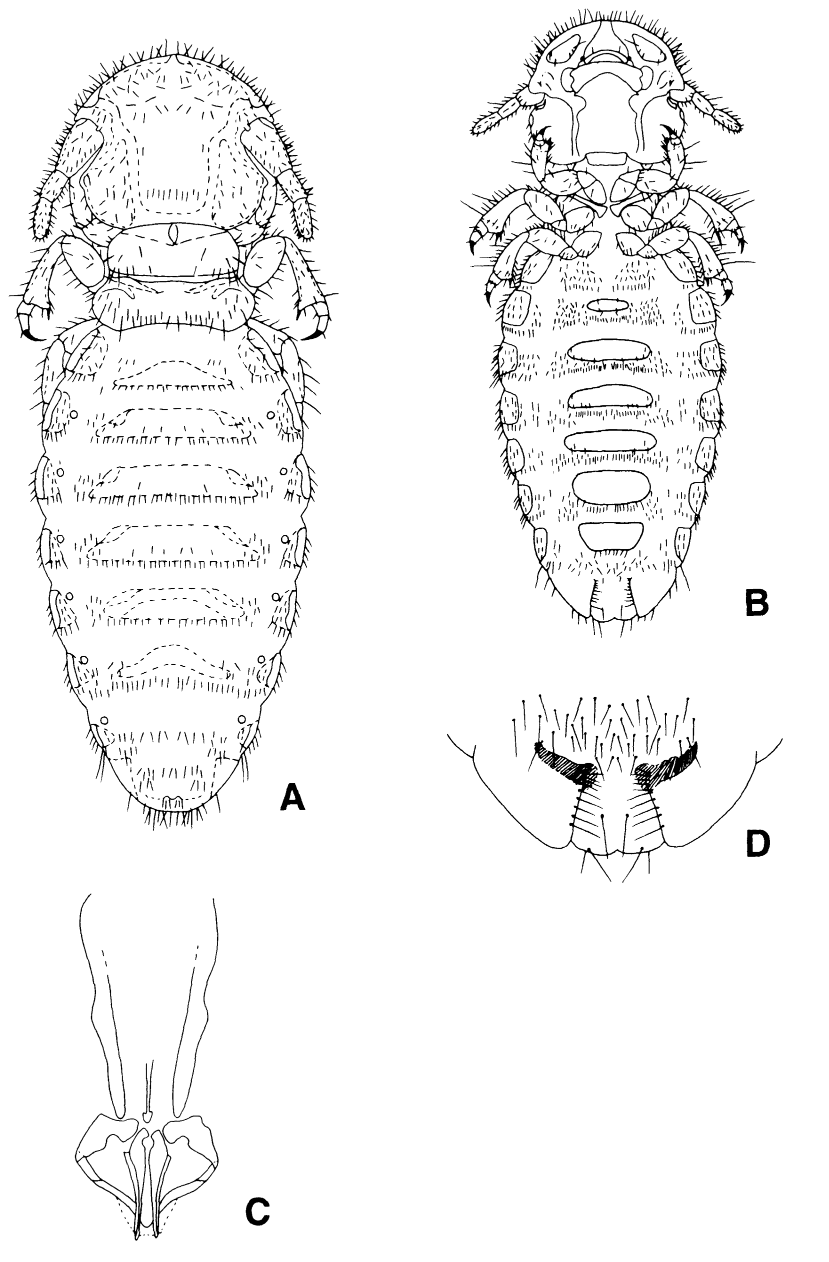


Figure 71. *Bovicola equi* (horse biting louse): ***A***, Dorsal view of male; ***B***, ventral view of female; ***C***, male genitalia; ***D***, female terminalia. Redrawn with minor modification by Wen Sam Wang from Emerson and Price (1975); courtesy of Brigham Young University Science Bulletin, Biological Series.

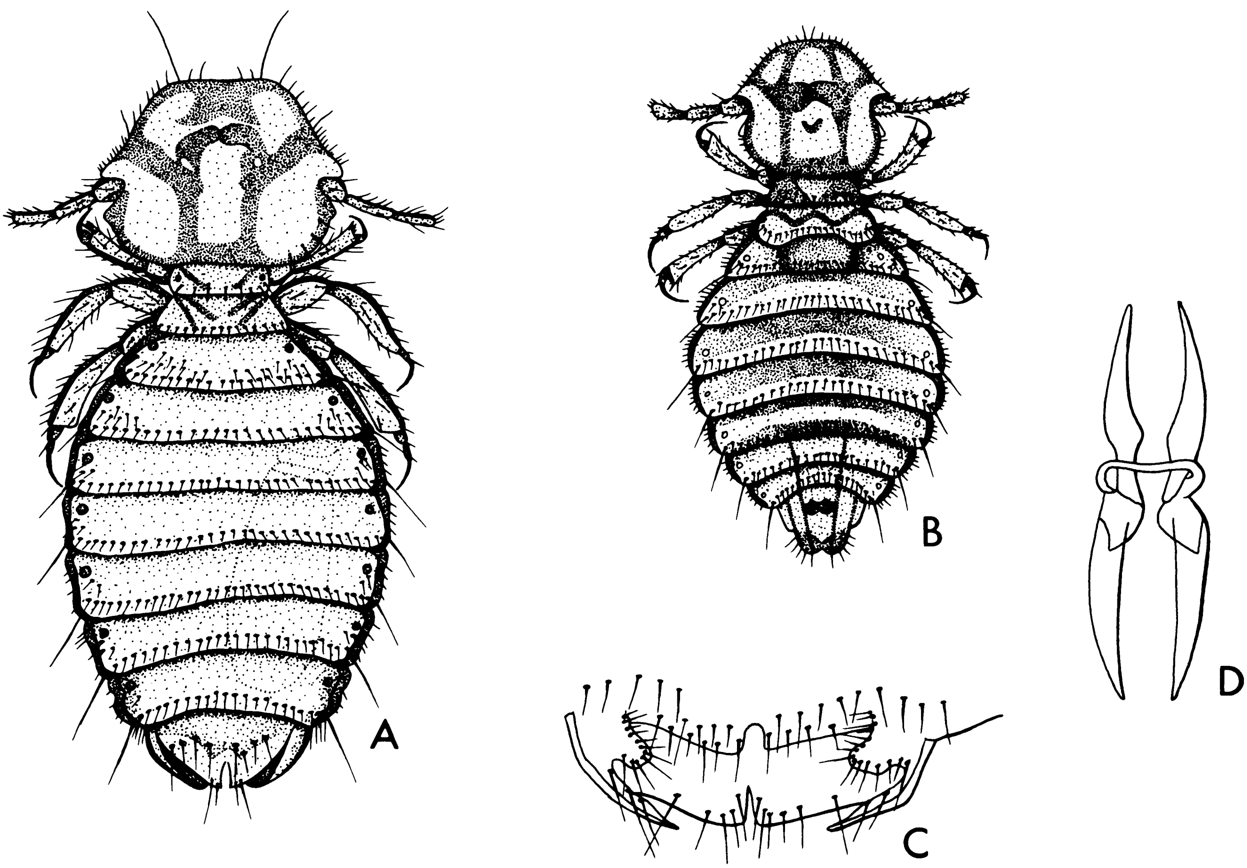


Figure 72. *Bovicola limbatus* (Angora goat biting louse): ***A***, Dorsal view of female; ***B***, dorsal view of male; ***C***, female terminalia; ***D***, male genitalia. Redrawn with minor modification by Jan Read from Morse (1903); courtesy of The American Naturalist.

Figure 73. *Bovicola limbatus*: Ventral view of adult. SEM × 50, by Theresa Droste; courtesy of Department of Entomology, Texas A&M University.

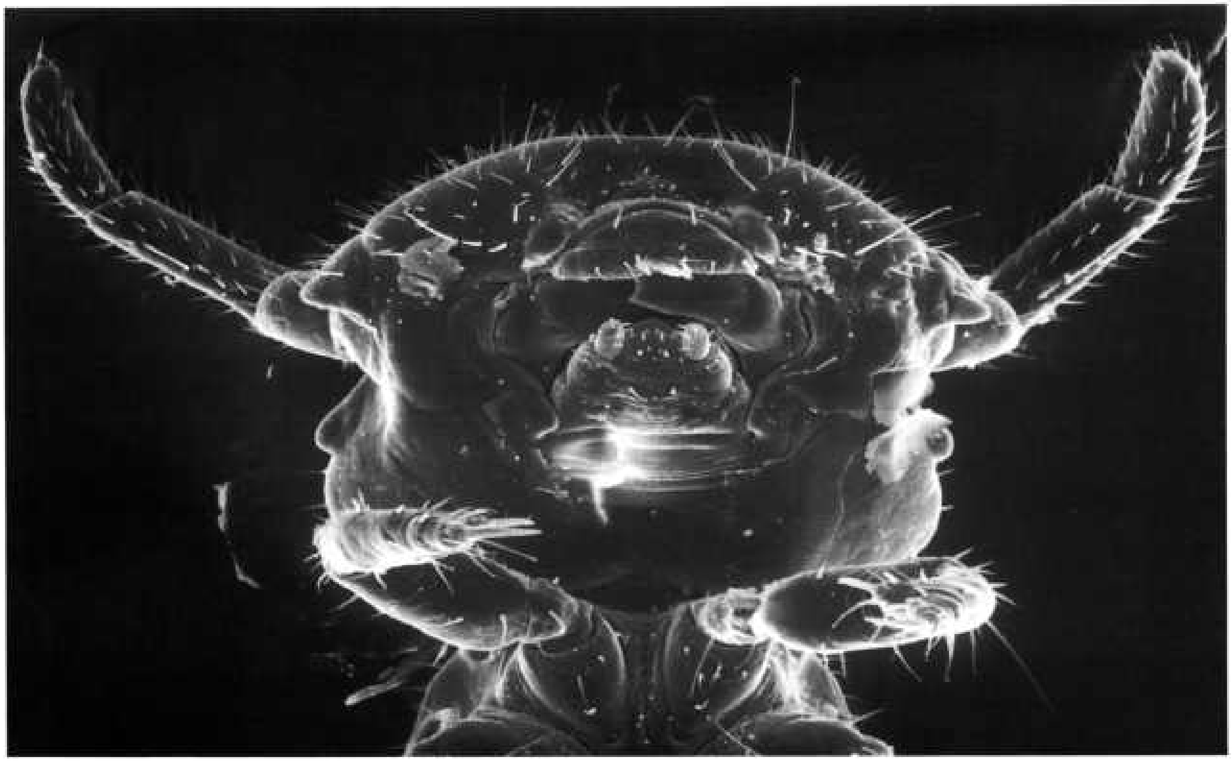


Figure 74. *Bovicola limbatus*: Underside of head of immature louse. SEM × 120, by Theresa Droste; courtesy of Department of Entomology, Texas A&M University.

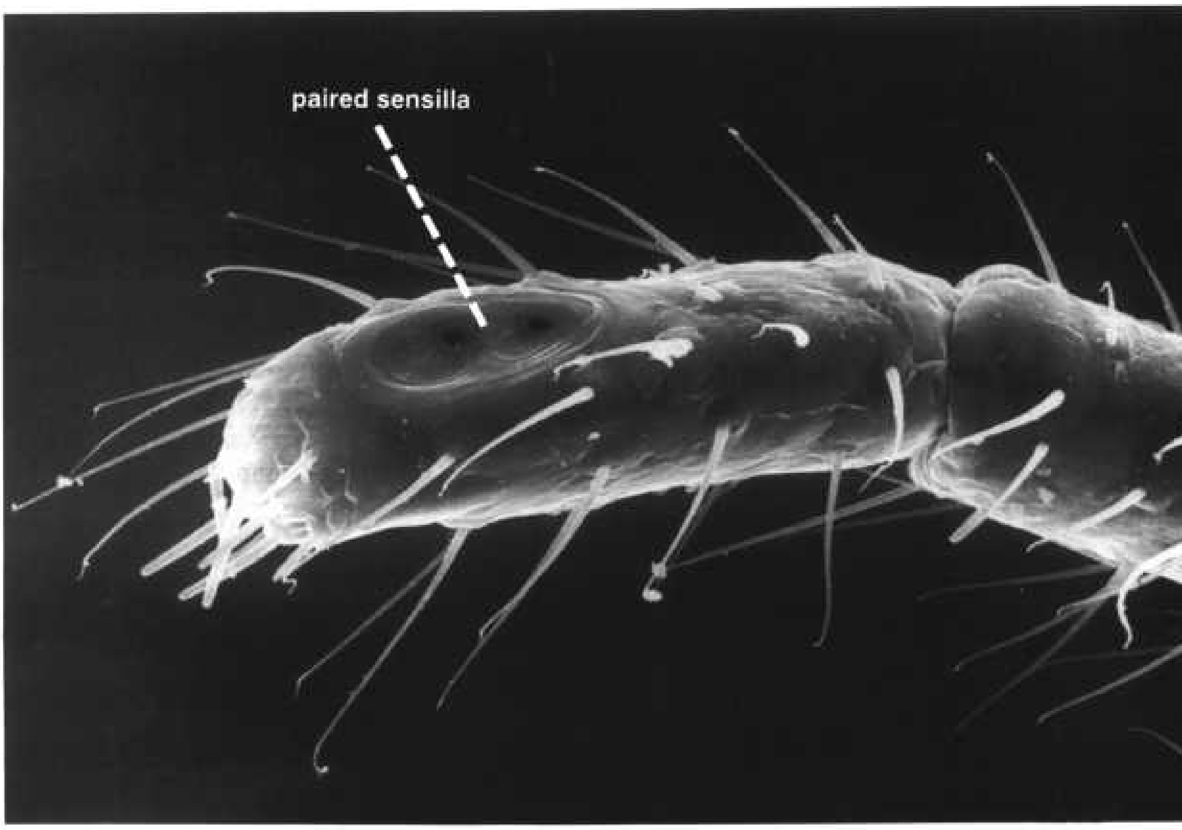


Figure 75. *Bovicola limbatus*: Terminal segment of antenna with its sensilla. SEM × 500, by Theresa Droste; courtesy of Department of Entomology, Texas A&M University.

(1950) reported its presence in Argentina, Brazil, Panama, Burma, and South Africa (Transvaal). It is found on all Angora goats, including kids in South Africa. In the United States, *B. limbatus* is the most common louse on Angora goats (Horak et al. 1991b). It is also found on Spanish goats—most frequently when Spanish goats are pastured with Angora goats.

The life history of *Bovicola limbatus* can be deduced from data provided by Hopkins and Chamberlain (1969), who reared it in vitro at 35 °C±1.5° and 76% relative humidity. Females cemented their eggs to a single mohair fiber, but about half the eggs were loose in the rearing vials. The hatch averaged 84%, and nymphs from 67% of eggs survived to the adult stage. The time required for development of the different stages is shown in table 5.

Table 5. Life cycle of *Bovicola limbatus* [a]

	Time (days) required for development	
Stage	**Range**	**Average**
Egg	9–12	9.8
1st instar	5–9	6.1
2d instar	4–9	5.3
3d instar, males	5–12	6.3
3d instar, females	5–9	6.6
Preoviposition	3.5–7.5	4.4
Adult longevity, males	9–41	21.0
Adult longevity, females	5–53	18.8

[a] Reared at 35 °C±1.5° and 72% relative humidity
Modified from Hopkins and Chamberlain (1969)

At the time of adult emergence, the ratio of males to females in the colonized lice was 1:1.7. A male-female ratio of 1:3 was maintained in the rearing vials. In a single trial, females isolated from males did not reproduce parthenogenetically. The average rate of egg laying was 0.8 eggs/days by females aged 4–15 days, but the rate declined in older females. The life cycle from egg to egg averaged 32.2 days.

Injuries to goats caused by the three species of chewing lice have not been clearly defined, but because the mohair on heavily infested Angora goats becomes ragged, matted, tangled, and discolored, its market value is reduced. There may also be a loss in the quantity sheared—as much as 0.5 lb of mohair per animal (Babcock and Cushing 1942b). Since 1950, losses have been greatly reduced by applying an insecticide to Angora goats once or twice per year, but the mohair producer must still pay the costs of the insecticide, its application, and animal handling.

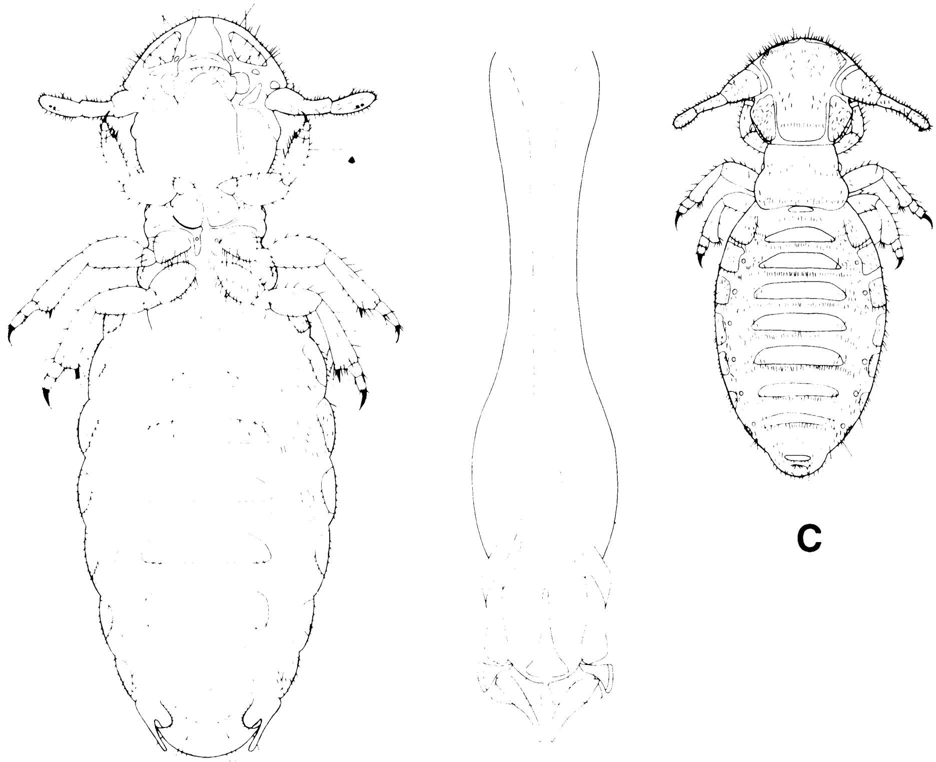
Bovicola ovis (sheep biting louse)

Other common names are used for *Bovicola ovis* (figs. 76, 77) in other countries. In Australia, Roberts (1952) called it the body louse and Scott (1952) the sheep body louse. In South Africa it is usually referred to as the red louse (Zumpt 1970) and in Canada as the red-headed sheep louse (Hearle 1938). This small, pale louse has a broad, reddish head. Females may be as much as 1.8 mm long, but males are much smaller—usually about 1.0 mm long.

The sheep biting louse apparently accompanied domestic sheep wherever they were carried and is now distributed worldwide. Werneck (1950) reported it from the United States, Brazil, Peru, and Uganda. Zumpt (1970) stated that sheep in the Transvaal province of South Africa were sometimes heavily infested. *B. ovis* is well known in Canada, Australia, and New Zealand (Hearle 1938). In Australia it is found in all of the sheep-raising regions but is scarce, sometimes even absent, in the drier inland areas (Roberts 1952). Lozoya-Saldaña et al. (1986) found it on sheep in Coahuila, Mexico, where its incidence was low. This louse was a common parasite of sheep throughout the United States in the early 1900's but was most abundant on range sheep in the western states (Imes 1928). Fragments of *B. ovis* were recovered during archeological excavations from deposits in Viking Greenland that dated back to A.D. 986 to 1350 (Sadler 1990).

Life history. As is true for other Mallophaga, all stages of *B. ovis* are found on the host, usually clasping a wool fiber with the first pair of legs and between the maxillary palpi and mandibles (fig. 78). Lice leave the host only to transfer to another sheep. Individuals that are lost from the host (as when they are rubbed off) perish unless they quickly find another host.

Females usually cement their eggs to wool fibers at a point about 6 mm from the sheep's skin, but eggs are also placed on hairs on the legs and other body parts of the sheep. If the fleece is thick and several inches long, the eggs may be placed at a greater distance from the body. The eggs are large in relation to the size of the female—about 0.8 mm, or half the length of the insect. Murray (1955b, 1957b) found that oviposition takes place only if the temperature of the microhabitat is suitable (37.5 °C±2.5°) and only if a fiber of suitable



A B C

Figure 76. *Bovicola ovis* (sheep biting louse): ***A***, Ventral view of female; ***B***, male genitalia; ***C***, dorsal view of male. Redrawn with minor modification by Wen Sam Wang from Emerson and Price (1975); courtesy of Brigham Young Science Bulletin, Biological Series.

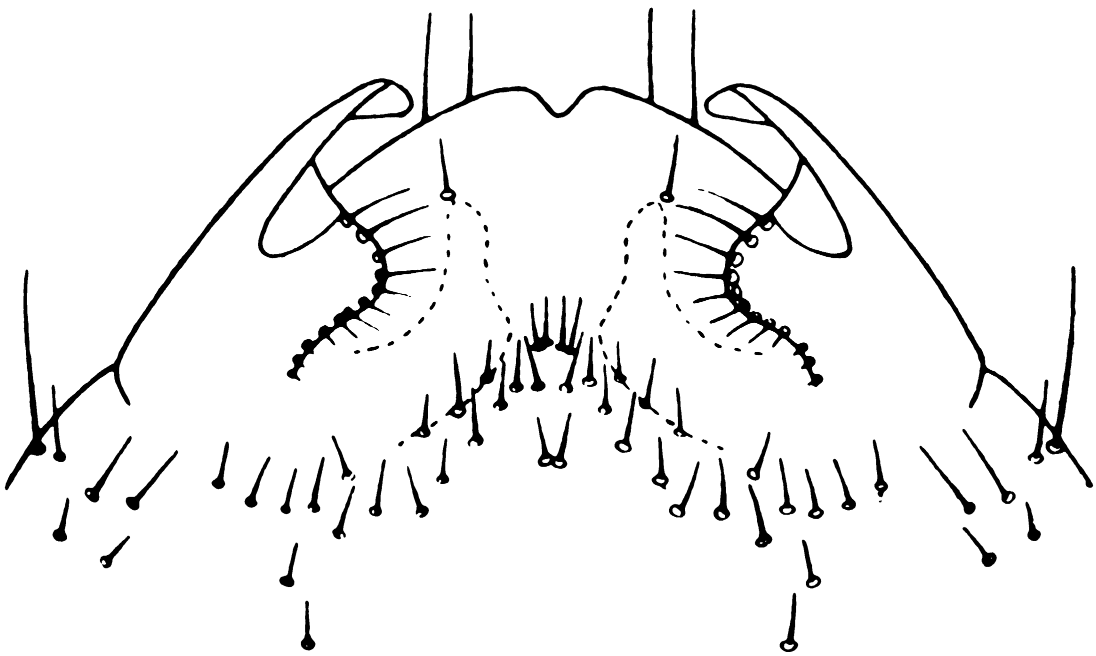


Figure 77. *Bovicola ovis*: Female terminalia. From Emerson and Price (1975), reprinted by permission of Brigham Young University Science Bulletin, Biological Series.

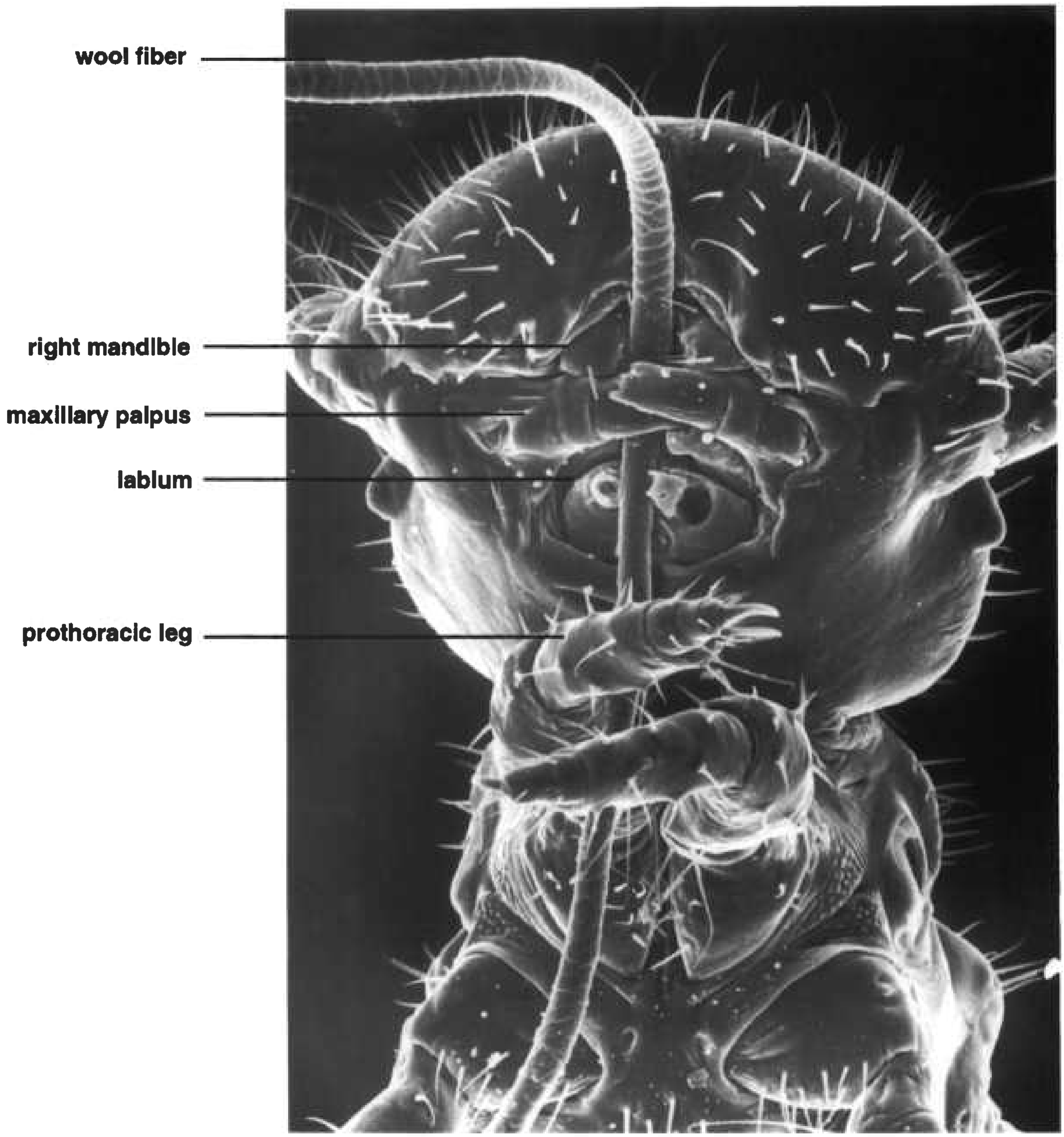


Figure 78. *Bovicola ovis*: Ventral view of head and prothorax. SEM × 130, by Theresa Droste; courtesy of Department of Entomology, Texas A&M University.

diameter is available. The wool fiber is clasped between a gonopod and the female's abdomen just prior to oviposition. Because the female turns just before depositing an egg so that the tip of the abdomen is pointing toward the sheep's body, all eggs are attached to the fiber with the base of the egg nearest the skin. Since there is a tendency to place one egg near another, clusters of eggs may be seen on heavily infested sheep. The eggs are always near the body of the sheep, are not exposed to wide fluctuations in temperature, and can be expected to hatch 8–10 days after oviposition.

Scott (1952) studied the life history of the sheep biting louse both on and off the host. Murray (1955b, 1957a, b,c, 1960b, 1963a,c, 1965, 1968) and Murray and Gordon (1969) expanded Scott's research into a series of studies on the ecology and behavior of *B. ovis*, which also yielded considerable bionomical data. Hopkins (1970) and Hopkins and Chamberlain (1972b) established a thriving laboratory colony of *B. ovis* and reported observations on its life history. The data presented by workers from different sides of the world agree quite well and were used by us in preparing the following composite summary of the life history.

Both nymphs and adults of *B. ovis* feed on epidermal scales, scurf, dried serum, suint, and other skin debris. All of the louse's nutitional requirements seem to have been satisfied by the dried scrapings of frozen sheepskin that Hopkins and Chamberlain (1972b) provided to their laboratory colony. At a constant temperature of 37 °C±2° and at 68% relative humidity, the life cycle is completed in 32–34 days. The time required for the development of the different stages is shown in table 6.

Although unmated female *B. ovis* deposited about the same number of eggs as mated females, none of the eggs from unmated females hatched; Hopkins and Chamberlain (1972b) concluded that this species does not reproduce parthenogenetically. Copulation was described by Clarke (1990) as follows: There are two large, posterior-facing hooks on the terminal segment of the male antenna. The male lies below and behind the female with the front of its head even with the metathoracic-abdominal region. The antennae are then turned up over the male's head to clasp the female about halfway along the abdomen. The tip of the male abdomen curls up to meet the terminal segments of the female, and insemination then occurs.

Females begin to oviposit about 4 days after molting and produce one egg about every 3–4 days throughout their lifetime, which averages 57 days. Scott (1952) reported a slightly higher rate of egg production: one egg every 2–3 days. This rate corresponds closely to the 0.45 egg/days reported by Hopkins and Chamberlain for females 7–14 days old. The latter authors noted that the male-female ratio in their colonies was 1:1.2. Newly emerged females mate soon (often less than 1 hr) after molting, but males are apparently not sexually mature until they are 2–4 hr old. A male can inseminate one to four females in 24 hr.

Table 6. Life cycle of *Bovicola ovis* [a]

	Time (days) required for development	
Stage	**Range**	**Average**
Egg	8.25–10.25	9.1
1st instar, males	5.25–8.25	7
1st instar, females	5.75–16.75	7.1
2d instar, males	5–7	5.7
2d instar, females	5–11	5.9
3d instar, males	6–9	7.3
3d instar, females	5–11	7.2
Preoviposition	3–4.5	3.9
Adult longevity, males	16–74	49.5
Adult longevity, females	5–53	27.7

[a] Reared at 37 °C±1.5° and 68% relative humidity
Modified from Hopkins and Chamberlain (1972b)

Fecundity of the sheep biting louse is low. Data from Hopkins and Chamberlain (1972b) can be used to calculate that in a laboratory colony, a female produces only 15 eggs in her lifetime. However, a favorable assumption used by Murray and Gordon (1969) in their population model indicates that on a sheep, a female may lay as many as 33 eggs. Even if the second statistic is accepted as correct, it can still be seen that an explosive buildup in population is not possible; for the number of lice on a sheep to reach the level of 0.4 to 1 million (as is sometimes seen in late winter), at least 4–5 mo of favorable weather must follow a date when a sheep is infested with at least 0.3 lice/cm^2 (2 lice/inch^2).

Niven (1985) concluded that if an average of 1 louse is seen each time the wool is parted, the sheep has approximately 5,000 lice on its whole body. Wilkinson et al. (1982) used a different system in their research; they parted the wool in several body areas a total of 40 times and recorded the number of lice counted. Their higher counts varied from 310 to 381 lice seen in 40 partings of wool.

Host-parasite relationships, ecology, and economic importance. For all practical purposes, *Bovicola ovis* is restricted to a single host: the domestic sheep. Werneck (1950) mentioned that *B. ovis* had also been collected from the Abyssinian black-headed sheep (now believed to be the same species as the domestic sheep) and from the mouflon (*Ovis musimon*). The latter record was obtained by Cummings (1916), who collected the lice in the Zoological Garden of London. Butler (1985) listed the bighorn sheep (*Ovis canadensis*) as a host.

Nymphs and adults of the sheep biting louse live in the rather stable air mass trapped by the fleece between the skin of the sheep and the tips of the wool fibers, the dermecos. The lice move freely through the fleece, and it appears that their movements are primarily governed by the need to situate themselves in a microhabitat whose temperature is suitable for feeding, growth, survival, and reproduction.

The skin temperature of a sheep is about 38 °C (Murray 1968); in a 1-yr study, Scott (1952) recorded a range of 36.1–38.6 °C. Murray (1957a) found that if the air temperature was 24.5 °C, temperature measurements made on a 1-inch-long fleece at intervals of 6.3 mm (¼ inch) from the body declined as follows: 37.5° (at skin), 34.75°, 33°, 30.5°, and 24.5° (at tip). In another observation in which the fleece was 4 inches long and the air temperature 20 °C, temperature measurements at intervals of 25 mm (1 in) from the body declined as follows: 37.5° (at skin), 35°, 31°, 28°, and 21 °C (at tip).

However, the skin temperature of sheep, like that of other animals, approximates air temperature if measured on the legs, especially the lower legs. When a sheep was placed in a cold chamber and held at 10 °C for several hours, the skin temperature measured at various places on the lower leg (fig. 79) varied from 11.5 to 12.5 °C (Murray 1957c). Conversely, during summer, the outer surface of the fleece may be much warmer than the skin, and the lice may move toward the skin to avoid unfavorably high temperature.

Both the lice and their eggs are killed by temperatures of 45 °C and higher. In summer, the temperature of the surface of the fleece may rise to 65 °C in a few minutes if the sheep is in bright sunlight. In addition, egg production declined more than 93% and eggs failed to hatch after lice had been exposed to 45 °C for 4 hr (Murray 1968). (However, when eggs were tested that had embryonated for 5 days at 37 °C, 100% mortality was observed for those eggs when exposed to 47 °C for 4 hr or to 49 °C for 1 hr.)

Sheep biting lice prefer to remain in the parts of the fleece that have a temperature of 37.5 °C±2.5°; that is the most favorable temperature for oviposition, feeding, growth, and development. Hopkins (1970) found that *B. ovis* in an in vitro colony held at a constant 37 °C produced seven times more eggs than did others held at 35 °C and three times more than those held at 41 °C. Both fecundity and hatch were significantly higher at 37 °C±1.5° than at 39 °C±1.5°.

Bovicola ovis is apparently less sensitive to fluctuations in the relative humidity of its habitat than to fluctuations in temperature. Exposure of nymphs and adults to 100% relative humidity for 24 hr did not cause high mortality (Murray 1963c), but immersion in water for 6 hr (such as when a fleece has been rain-soaked) was lethal. Embryonic development proceeds normally in the range of 7% to 92% relative humidity, and egg hatch was not impeded by humidities of 7%–75% but was greatly reduced when eggs were held at 92% relative humidity for the last 24 hr preceding hatch (Murray 1960b). In the laboratory, fewer eggs were produced by lice held at 95% relative humidity than by those held at 60% or 20% (Murray 1957b). Murray (1960b) considered the combination of 37 °C and 54% relative humidity to be "near optimum" for the survival of sheep biting louse.

Since a rain-soaked fleece remains wet for many hours, periodic rains can cause considerable mortality of sheep biting lice, and autumn rains may reduce louse populations to such a low point that the sheep are only lightly infested the following winter and spring (Murray 1963c).

In the laboratory, female *B. ovis* oviposit as readily on a synthetic fiber (for example, a $1\frac{1}{2}$ denier strand of nylon) as on a natural fiber. However, the lice use only fibers that are about 0.02 mm in diameter, because they must be able to clasp the fiber between a gonopod and the abdomen in order to attach the egg (Murray 1957b). Suitable fibers—either hairs or strands of wool—are available over most of the sheep's body, even the hairy parts. Consequently, fiber diameter plays very little part in determining the lateral distribution of *B. ovis* on sheep (Murray 1957c).

In summer, females may oviposit on the body extremities if skin temperatures are cooler and thus more favorable than those on the back and upper sides of the sheep. The distribution of lice on the sheep's body in summer differs somewhat from winter distribution; Roberts (1952) mentioned that at times, large numbers of *B. ovis* could be found on the underside of the neck in summer.

Kettle and Pearce (1974) in New Zealand made 8 monthly counts of the number of *B. ovis* in each of 13 body regions and found that in winter, when the lice were most abundant, the largest numbers (65% of total) were found in the 6 regions of the upper body. In late spring, lice were almost completely absent from those regions; the small numbers that were found were in the

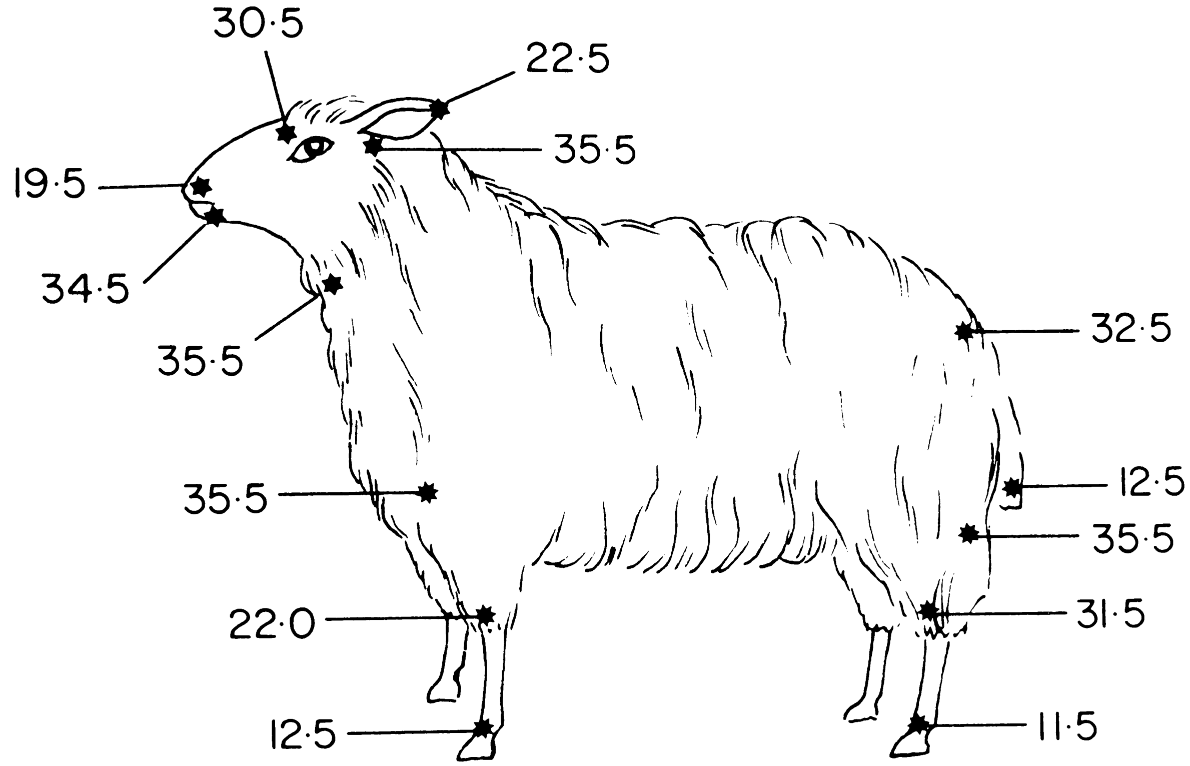


Figure 79. Temperatures on various areas of skin when a sheep is held at 10 °C. From Marshall (1981), The Ecology of Ectoparasitic Insects, reprinted by permission of Academic Press Ltd, London.

wool on the ribs, lower flank, and abdomen. When populations of *B. ovis* are high, usually in winter, most of the lice are found on the back and midsides of the sheep. Within the fleece, most lice stay near the skin (usually within 6 mm) in the optimum temperature zone; that is where the eggs are deposited and where both nymphs and adults are presumed to do most of their feeding. However, many of the lice (perhaps as many as one-fourth of the total) can be found farther from the skin, randomly scattered throughout the wool. Sheep shearing can cause the loss of 35%–50% of lice that are present in spring and can render the microclimate of the remaining 6 mm of wool unsuitable for lice (Murray 1968, Marshall 1981).

If not inhibited by cold, the lice readily move to the outer surface of the fleece but do not remain there unless it is shaded, because they are negatively phototactic. If a cloth is placed on the fleece of a heavily infested sheep (especially if the cloth is warm), lice will transfer readily to the undersurface of the cloth. There the lice continue to avoid bright light; if the cloth is carried into the laboratory, they move away from a light source (such as a window) and crawl into folds of the cloth.

The spread of *B. ovis* from sheep to sheep is believed to take place when two or more sheep are in close contact with one another. Scott (1952) noted that lambs were infested soon after birth by lice that transferred from their mothers. Because lice that are not on a host seldom live more than 5 days—even when they are on a tuft of wool and ambiental conditions are favorable for survival—it seems that the risk of clean sheep acquiring lice from premises previously occupied by lousy sheep is very low.

Since old sheep and those in poor health seem to be more susceptible to louse infestation than are strong, healthy sheep, Scott (1952) tested the effects of host nutrition on the winter increase of louse numbers by artificially infesting two groups of crossbred sheep—one well fed and the other poorly fed—with equal numbers of *B. ovis.* In that experiment, lice multiplied rapidly on only the poorly fed animals; but in another trial in which Merino sheep were used, both groups became heavily infested.

Nevertheless, it is generally believed that poorly fed sheep are more susceptible to lice and that they may be infested with appreciable numbers of *B. ovis* year-round (Graham and Scott 1948, Roberts 1952). In the case of sheep on good feed, Kettle and Pearce (1974) concluded that low-to-moderate infestations of *B. ovis* did not cause reductions in weight gain. Murray (1963c, 1965) calculated that a heavily infested sheep may carry as many as 0.5 to 1 million sheep biting lice.

The sheep biting louse apparently feeds on epithelial scales and other skin scurf. Scott (1952) used skin scrapings as food for a laboratory colony, and Hopkins and Chamberlain (1972b) reared *B. ovis* for 25 generations on sheepskin scrapings. Other investigators have suggested that bits of wool may also be used as food, but Waterhouse (1953) doubted that this insect is physiologically capable of digesting wool and further noted that wool is seldom ingested. Zumpt (1970) stated that lice irritate the skin of sheep sufficiently to cause the secretion of tissue fluids (which he referred to as serum) and that sheep biting lice feed on the dried fluids. Zumpt also said that the wool on lousy sheep is sometimes matted by dry serum. Scott found that in the laboratory, *B. ovis* that were given dry serum as food lived only about half as long as others that were fed skin scrapings. Hopkins and Chamberlain observed that *B. ovis* would feed on scrapings from goatskin and cowhide but that adult survival, fecundity, and egg hatch were drastically reduced compared with those values for lice fed on sheepskin scrapings.

Apparently the sheep biting louse causes measurable economic losses when the louse population is quite high, but severe injury is usually restricted to a few older sheep or those in a weakened condition. Zumpt (1970) described a sequence of events that culminated in severe outbreaks of *B. ovis* in several flocks of sheep in two districts of South Africa. In essence, mild winter weather occurred when grazing was poorer than usual because a summer drought had left the pastures with mostly unpalatable forage plants; this resulted in louse buildup in the weakened animals, which then caused matted wool and loose strands of pulled-out fleece, and finally resulted in economic losses. Several observers have agreed that heavily infested sheep react to lice by rubbing on a solid object such as a tree or post and by biting or scratching; this behavior damages the fleece and reduces its value (Waterhouse 1953; Wilkinson 1977, 1978; Kettle 1984; Butler 1985). The wool becomes ragged and its quality is reduced, caused in part by the increased content of dirt, bark, and other foreign materials in the fleece. Severely infested sheep may be seen with large areas of wool rubbed off and sores on the bare areas (Price et al. 1967b). In a flock, certain sheep seem to be highly sensitive to louse irritation and react more vigorously than the other sheep (Sinclair 1976).

The importance of louse control was recognized long ago by sheep raisers in Australia and New Zealand, where for many years control was mandatory and was supervised by government inspectors (Graham and Scott 1948, Shanahan and Wright 1953, Kettle and Pearce 1974, Heath and Bishop 1988). A sheep louse detection test is used in Western Australia to search for *B. ovis* in wool that is stored in warehouses (Morcombe 1992);

any positive samples can be traced back to the flock from which the wool was sheared.

The loss of wool caused by the reaction of sheep to moderate-to-heavy louse infestation was calculated by Wilkinson (1977, 1978) to be about 0.5 kg/animal. He found that losses caused by sheep lice, both chewing and sucking, in the state of Western Australia totaled A$8 million annually. It was also calculated that if a fleece had a potential value of A$5, reductions in value of A$0.30, $0.70, and $1.40 would occur if the fleece were sheared from light, medium, and heavily infested sheep, respectively (Western Australia Department of Agriculture 1978). Wilkinson et al. (1982) found that in Western Australia, louse infestation reduced the production of clean wool by 0.3–0.8 kg/animal; this wool had a value of A$0.72 to $1.92. Niven (1985) calculated that wool from louse-infested sheep was worth A$0.72–$3.19 less per fleece than wool from louse-free sheep.

Other species of *Bovicola*

In addition to the six species of *Bovicola* that parasitize domestic animals, another 11 species parasitize large North American game animals, either native or introduced. *Bovicola breviceps* is a parasite of llamas and their relatives, and has been collected at the Zoological Garden of Washington (District of Columbia) as well as in South America (Werneck 1950). Two species, *Bovicola concavifrons* and *B. longicornis*, have been recorded from American elk (wapiti), but the type host for *B. longicornis* is the red deer of Europe, *Cervus elaphus*. (Some authorities consider wapiti and red deer to be a single species.) Sleeman (1983) reported that in Ireland, *B. longicornis* had been collected from red and sika deer. Both lice seem to be parthenogenetic, with males only rarely recorded (Hopkins 1960). The aoudad or Barbary sheep (*Ammotragus lervia*), an introduced species in North America, is now well established in the United States and is host for *Bovicola fulva* and *B. neglectus* (Emerson and Price 1979). *Bovicola jellisoni* is a parasite of the bighorn sheep (*Ovis canadensis*) (Emerson 1962a) and Dall's sheep (*Ovis dalli*) (Kim 1977). *Bovicola ocellata* is a parasite of Burchell's zebra (*Equus burchelli*); it has apparently transferred to the domestic donkey and is now found on that host in North America (Kim et al. 1990).

Still another species, *Bovicola oreamnidis*, has been collected from the mountain goat, *Oreamnos americana* (Hopkins 1960). The type host for *Bovicola sedecimdecembrii* is the European wisent (*Bison bonasus*), but the same louse is found on American bison (*Bison bison*). *Bovicola tarandi* parasitizes both the Old World reindeer and its close relative, the New World caribou; Low (1976) reported severe infestation of one caribou and light-to-moderate infestation of four others. Westrom et al. (1976) reported the transfer of *Bovicola tibialis* from introduced fallow deer (*Dama dama*) to native black-tailed deer (*Odocoileus hemionus*). Because no male lice were found in collections that totaled over 18,000 female lice, the authors suggested that parthenogenetic reproduction occurs. Sleeman (1983) noted that *B. tibialis* had been recorded from fallow deer in Ireland.

Genus *Trichodectes*

Trichodectes are robust, have a broad head, and are with or without a wide, shallow notch on the anterior margin. The antennae are three-segmented and may or may not be sexually dimorphic. Clay (1970) has illustrated the antennal sense organs of *Trichodectes melis* (fig. 80). The prothorax is distinct from the pterothorax and is somewhat larger. The legs are well developed with a single well-developed claw on the distal end of the tarsus. In both sexes the abdomen is broad and oval, and stigmata are present. Long abdominal bristles are arranged in single transverse rows on the terga, sterna, and pleura. The last abdominal segment of the male forms a caudal projection. The gonapophyses have smooth inner margins, are without lobes, and appear to be linked to the subgenital lobes by a series of bristles arranged in an arc and usually set on pedestals (Wiseman 1959).

Werneck (1948) listed 12 species worldwide, but Hopkins and Clay (1952, 1953, 1955) increased the number to 31 by including *Neotrichodectes* and *Stachiella* as subgenera of *Trichodectes*. Emerson and Price (1981) chose to recognize 14 species of *Trichodectes* plus 1 subspecies from bears, badgers, raccoons, and dogs; 10 species of *Neotrichodectes* from skunks, badgers, ringtails, and their relatives; and 9 species of *Stachiella* plus 3 subspecies from weasels and their relatives in the mammalian family Mustelidae. Emerson (1972a) listed three species of *Trichodectes* from North America north of Mexico.

Trichodectes canis (dog biting louse)

The head of *Trichodectes canis* is flattened, somewhat quadrangular, and wider than long, and it possesses short, thick antennae (fig. 81). The adults are yellowish with dark markings and 1–2 mm long. Although cosmopolitan in distribution, this species is uncommon in the United States.

The type host is the domestic dog, but Emerson (1972a) also listed the coyote (*Canis latrans*), the red wolf (*Canis niger*), and the gray wolf (*Canis lupus*) as other North American hosts. Emerson and Price (1981) added the African civet (*Viverra civetta*), the Asiatic jackal (*Canis aureus*), the Bengal fox (*Vulpes bengalensis*), a South

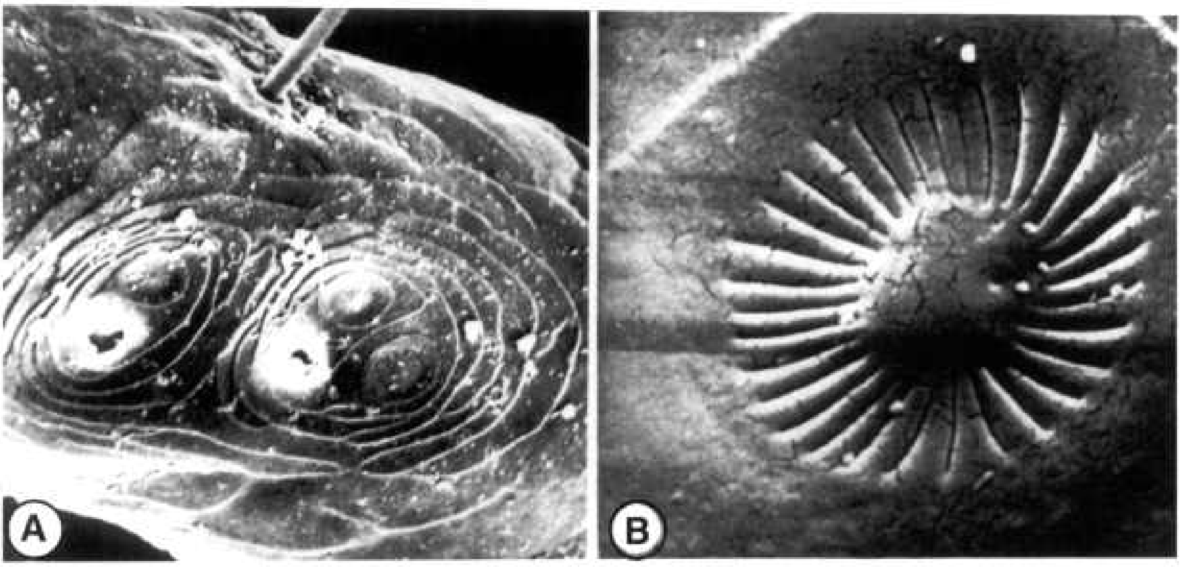


Figure 80. *Trichodectes melis*: Antennal sense organs. ***A***, Terminal segment of antenna (SEM × 1,300); ***B***, closer view of a single sensillum (SEM × 10,334). From Clay (1970), reprinted by permission of publisher. © British Museum (Natural History), 1970.

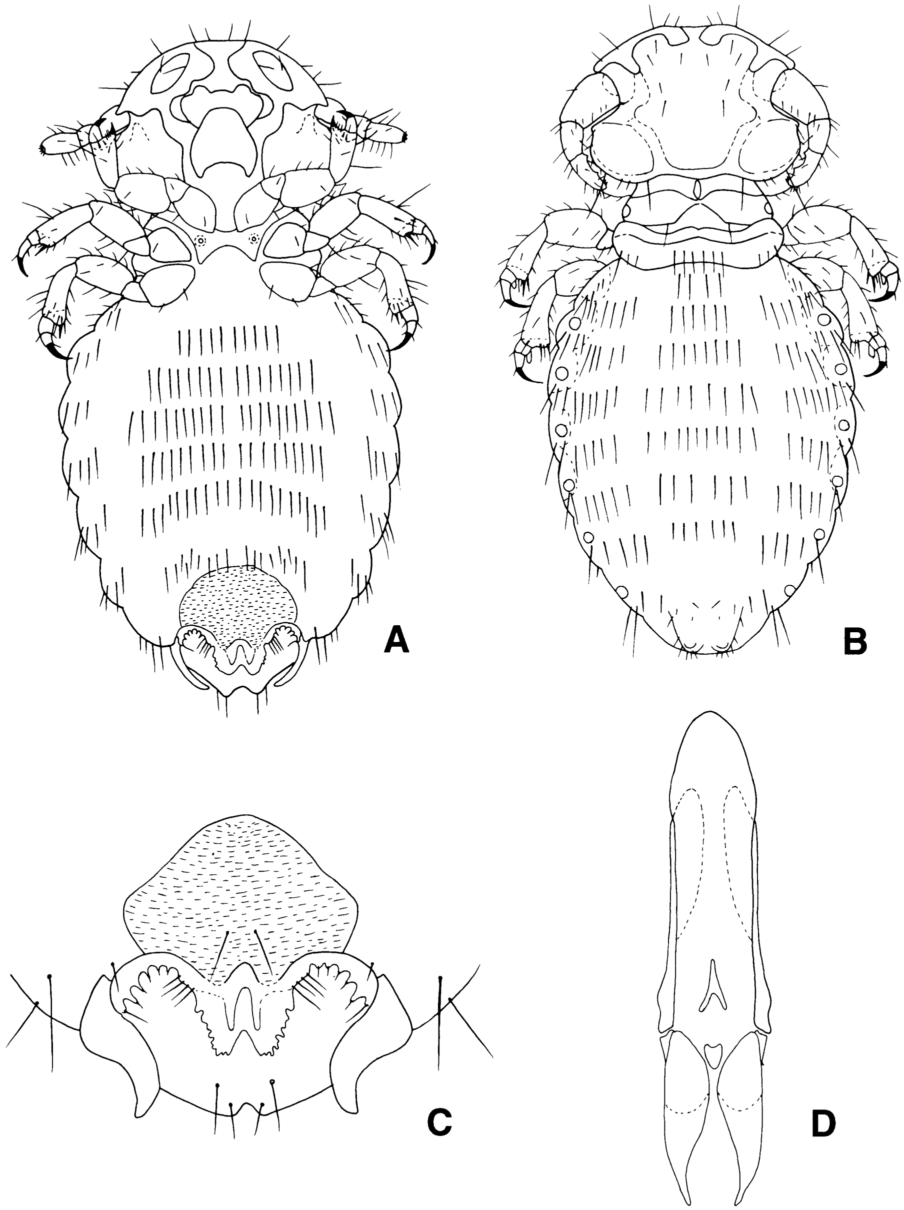


Figure 81. *Trichodectes canis* (dog biting louse): ***A***, Ventral view of female; ***B***, dorsal view of male; ***C***, female terminalia; ***D***, male genitalia. Redrawn with minor modification by Wen Sam Wang from Emerson and Price (1975); courtesy of Brigham Young University Science Bulletin, Biological Series.

American fox (*Dusicyon culpaeus*), and the savannah fox (*Cerdocyon thous*) as additional hosts.

Life history. The eggs are cemented to the base of a hair and hatch 7–14 days later. The nymphal stages require another 14 days or so to complete their development. Crystal (1949) has described the three nymphal stages. After being fertilized, the female may deposit one or more eggs per day for the remainder of her life. The period from egg to egg is approximately 30 days (Dement 1965). The louse feeds on tissue debris and will survive only 3–7 days if separated from its host (Kim et al. 1973).

Host-parasite relationships. The dog biting louse prefers the head, neck, and tail of its host, and these sites are usually more severely infested. This louse sometimes concentrates around wounds and body openings to feed on fluids. *T. canis* was reported by Bouvier (1945) to take blood meals, and it is the only member of the family known to do so (Lyal 1985). It is usually spread by direct contact of the hosts but may also be acquired from infested bedding, brushes, combs, and other accessories.

Signs of louse infestation in dogs were described by Sosna and Medleau (1992b). Lice cause intense irritation, inflammation, and pruritis through their blood feeding and movement on the skin's surface. The animal's scratching frequently causes secondary bacterial infection (Sosna and Medleau 1992a). Infested dogs rub, scratch, and bite the infested area and have a rough, matted coat. Lice are more abundant on very young or very old dogs in poor condition (Kim et al. 1973). Coyotes may be heavily infested with *T. canis*, but louse injury may be confused with mite-induced mange. Foreyt et al. (1978) described a coyote infested with an estimated 50,000 lice; host response to the lice had resulted in loss of much of its hair, and the remaining hair was sparse and matted. Also, the skin had been injured.

T. canis is an intermediate host for the double-pored tapeworm (*Dipylidium caninum*). This parasite of dogs, foxes, and cats occasionally infects humans (especially children) (Olsen 1974) (also see p. 11).

Other species of *Trichodectes*

Emerson (1972a) listed *T. pinguis euarctidos*, a parasite of the black bear (*Ursus americanus*), and *Trichodectes octomaculatus*, a parasite of the racoon (*Procyon lotor*), as occurring in North America. Pung et al. (1994) frequently collected *T. octomaculatus* from racoons in southeastern Georgia. Manville (1978) examined 113 black bears in northern Wisconsin and found lice on only 4 bears, but his examinations were made in summer. Two of the four infested bears were heavily infested; one of those was infested with approximately 5,000 *T. pinguis euarctidos* and was in poor physical condition.

Trichodectes ermineae was recovered from (mostly) road-killed Irish stoats (a subspecies of the weasel *Mustela ermineae*) by Sleeman (1989). The stoats, 46% of which were infested, were hosts for 1–27 lice per infested stoat. Males had more lice than female weasels, and the maximum infestation was recorded in summer. The Old World badger, *Meles meles*, is the host of *Trichodectes melis* (Emerson and Price 1981). Perez-Jimenez et al. (1990) found the louse to be abundant on badgers in southern Spain and generally distributed over their bodies.

Genus *Damalinia*

Many Europeans regard *Bovicola* as a subgenus of *Damalinia*, but we follow the American practice of separating the two genera. In appendix A we have listed 17 species (one has two subspecies) of *Damalinia*, which parasitize large mammals in the families Bovidae, Cervidae, and Tragulidae. *Damalinia* is restricted in its distribution to Africa (Ewing 1936). Horak et al. (1989) collected *Damalinia natalensis* from bushbuck (*Tragelaphus scriptus sylvaticus)* in South Africa, and Horak et al. (1992a) collected a small number of *Tricholipeurus antidorcas* (=*Damalinia antidorcas*) from the springbok (*Antidorcas marsupialis*) in national parks in Namibia.

Genus *Felicola*

By including *Suricatoecus*, *Neofelicola*, and *Parafelicola* as subgenera, Hopkins and Clay (1952) recognized 35 valid species of *Felicola*. Emerson and Price (1981) listed 23 species of *Felicola* plus 1 subspecies, but they recognized Hopkins and Clay's subgenera as valid genera. Perez-Jimenez et al. (1990) formed the new combination *Felicola (Suricatoecus) vulpis* for the louse from the Old World red fox (*Vulpes vulpes*).

The *Felicola* have a triangular forehead with the sides almost straight from the apex to the point of insertion of the antennae. The antennae are small to medium, three-segmented, and not sexually dimorphic. There is a narrow hair groove on the ventral surface of the head. The temporal lobes are rather abruptly rounded and almost square. The abdomen is small and the segments have pleural plates. Three pairs of abdominal spiracles are present. The genital plate is broad and poorly sclerotized. The parameres are narrow and almost straight.

Felicola subrostratus (cat louse)

Adults of *Felicola subrostratus*, the cat louse (fig. 82), are light yellow to tan and quite small. Males are slightly less than 1 mm long, and females average about 1.2 mm long (Eduardo et al. 1977). The head is pointed, with a median longitudinal groove on its underside. The abdomen is short and broad, and has three pair of spiracles and a sparse, fine, transverse row of minute dorsal hairs across each segment (Roberts 1952, Renaux 1964, Kim et al. 1973).

Felicola subrostratus is apparently cosmopolitan in distribution, but infested cats are only occasionally seen in the United States, Canada, Australia, India, and the Philippines (and perhaps all over the world) (Werneck 1948, Ansari 1951, Roberts 1952, Hopkins 1960, Eduardo et al. 1977). Roberts noted that the louse is most frequently seen on older, long-haired cats that are unable to clean themselves.

Life history. The eggs are laid on the cat's hair and hatch in 10–20 days. The immature stages require 2–3 wk for their development (Renaux 1964). The adults live and deposit eggs for another 2–3 wk.

Host-parasite relationships. The cat louse has been collected from several hosts (appendix A), most of which occur naturally only in the Old World. The domestic cat is the type host but may not be the host to which the louse is best adapted. Almost nothing is known about the life history of *Felicola subrostratus* on its wild hosts. It feeds on skin debris and perhaps on skin exudates that accumulate in breaks in the skin. This feeding causes the host to be restless, to lose appetite, and to show signs of general cutaneous irritation. The hair coat may be matted and have a ruffled appearance, due in part to the accumulation of skin exudates in the hair. The skin may show signs of redness and lacerations caused by scratching (Renaux 1964).

Other species of *Felicola*

The three other species of *Felicola* known from North America are *Felicola felis* from the mountain lion (*Felis concolor*) and the ocelot (*Felis pardalis*), *Felicola spenceri* from the lynx (*Felis canadensis*), and *Felicola americanus* from the bobcat (*Felis rufa*). Emerson and Price (1983) described as new the following species from Neotropical cats: *Felicola braziliensis* from the pampas cat (*Felis colocola*), *Felicola similis* from the jaguarondi (*Felis jaguarundi*), *Felicola sudamericanus* from the little spotted cat or tiger cat (*Felis tigrina*), and *Felicola neofelis* from Geoffroy's cat (*Felis geoffroyi*). Almost nothing is known about the life history of these lice; several have been collected only once or twice. The 20 remaining species of *Felicola* are known only from mongooses, civets, and their relatives from Africa, Europe, and Asia.

Genus *Tricholipeurus*

The head is notched anteriorly and is longer than broad in *Tricholipeurus*; the preantennal region is trapeziform or subtriangular, depending on the width of the antennal fossae. The antennae of many species show little or no sexual dimorphism. The thorax is not modified, and the sides of the abdomen are almost parallel, with strongly pigmented sternal, pleural, and tergal plates (Bedford 1929). The median lobes of the female genital region are greatly expanded. Gonapophyses are of typical trichodectid form and are not attached at their extremities. The copulatory apparatus consists of a basal plate with a median sclerite and also two small, free parameres and endomeres; it is without a pseudopenis (Wiseman 1959).

The number of valid species worldwide has changed little from the 23 listed by Werneck (1950). Emerson and Price (1981) listed 21 species; most were from bovids and cervids in Africa and Asia. Bedford (1932a) observed that *Tricholipeurus* are parasites of antelopes and deer. In the New World, in addition to two species from North American deer, Emerson and Price listed *Tricholipeurus albimarginatus* from neotropical brocket deer (*Mazama americana* and *Mazama gouazoubira*) and *Tricholipeurus dorcephali* from the pampas deer of South America (*Ozotoceros bezoarticus*) (see appendix A).

Tricholipeurus lipeuroides

Adult males and females of *Tricholipeurus lipeuroides* are slender lice that measure 2.5–2.75 mm long. The antennae are markedly sexually dimorphic. The male head is considerably wider across the forehead than across the temples (fig. 83). The male genitalia are conspicuous, with the basal plate consisting of two chitinous bars that reach the fifth abdominal segment. The parameres are free distally, long, tapering, and fused at their base; they are overlaid with a dorsal two-pronged chitinization. A median bilobed plate is present on the last abdominal segment of the female (Wiseman 1959).

This species is widespread in North America north of Mexico. Walker and Becklund (1970) listed records from 19 states in the United States and also 3 Canadian provinces. It has at least a limited distribution in the Neotropical Zoogeographical Region, because it was described from specimens collected in Mexico (Anderson 1962). The white-tailed deer is the type host, but the mule deer is an equally suitable host.

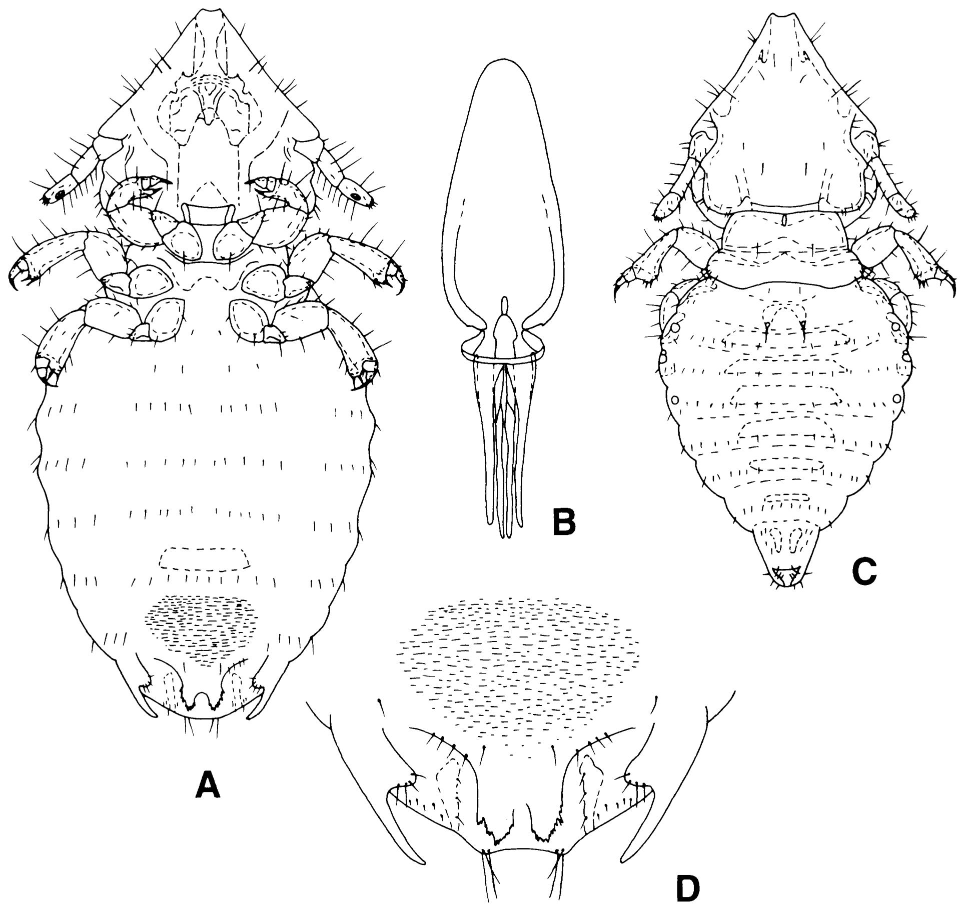


Figure 82. *Felicola subrostratus* (cat louse): ***A***, Ventral view of female; ***B***, male genitalia; ***C***, dorsal view of male; ***D***, female terminalia. Redrawn with minor modification by Wen Sam Wang from Emerson and Price (1975); courtesy of Brigham Young University Science Bulletin, Biological Series.

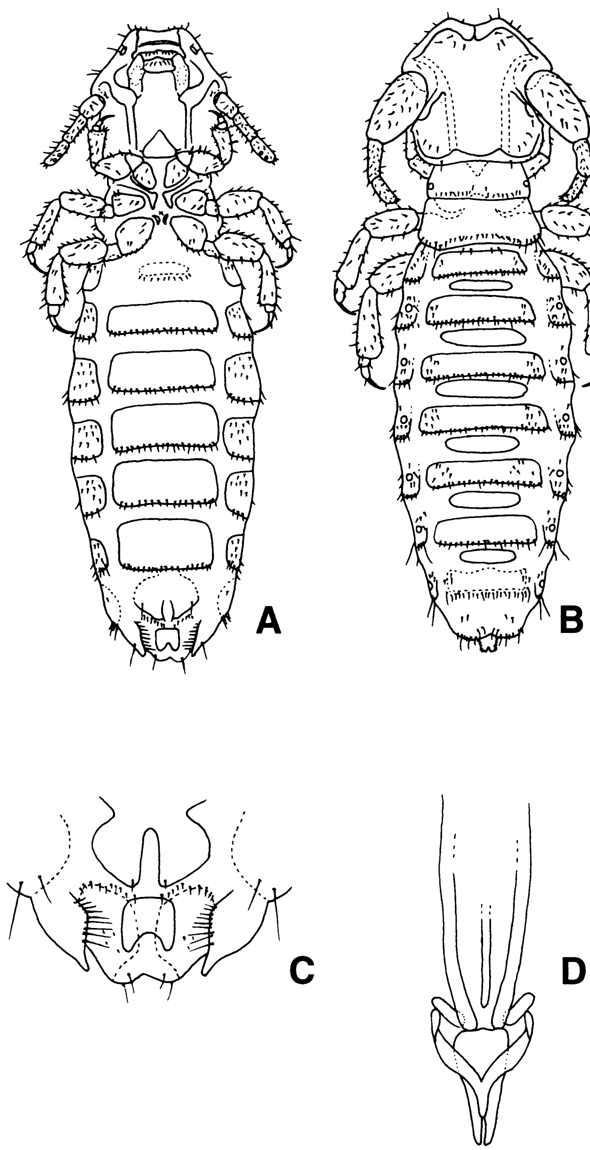


Figure 83. *Tricholipeurus lipeuroides*: ***A***, Ventral view of female; ***B***, dorsal view of male; ***C***, female terminalia; ***D***, male genitalia. Redrawn with minor modification by Jan Read from Werneck (1950); courtesy of Memórias do Instituto Oswaldo Cruz, Rio de Janeiro, Brazil.

The life cycle is unknown, but seasonal changes in the number on white-tailed deer in Ontario (Watson and Anderson 1975) are similar to those reported for chewing lice on domestic animals. Many more adult *T. lipeuroides* were counted in winter than in summer; seasonal changes in the number of immature lice followed the same pattern but were confounded by the occasional presence of mixed populations of immature *T. lipeuroides* and *T. parallelus* (immatures of the two species are not distinguishable).

Van Volkenberg and Nicholson (1943) associated gross infestations of *T. lipeuroides* with poor physical condition of Texas white-tailed deer in February. But Samuel et al. (1980) found that 8 apparently healthy white-tailed deer in Canada were each infested with 14,000–70,000 chewing lice.

Tricholipeurus parallelus

Sexual dimorphism of the antennae is not pronounced in *Tricholipeurus parallelus* (fig. 84), and the species is smaller than *T. lipeuroides*. Dark spots are present in front of the abdominal stigmata on each segment. The pseudopenis is V-shaped and without the pointed posterior projection that is characteristic of *T. lipeuroides*.

T. parallelus parasitizes both white-tailed and mule deer (appendix A), and its distribution in the United States and Canada appears to be the same as that of its hosts. Emerson and Price (1975) suggested that the louse probably also occurs in the Neotropical Zoogeographical Region. Concurrent infestations of *T. parallelus* and *T. lipeuroides* on both species of deer have been reported (Samuel et al. 1980), but they appear to be uncommon because Samuel and Trainer (1971) examined 434 white-tailed deer at one location in Texas and found only *T. parallelus* while other workers at nearby locations found only *T. lipeuroides* (Hightower et al. 1953, Van Volkenberg and Nicholson 1943). Hopkins (1960) corrected a misdetermination of "some specimens from the black-tailed deer (Baker collection)" by Osborn (1896) as *Trichodectes tibialis*; these specimens were actually *T. parallelus*.

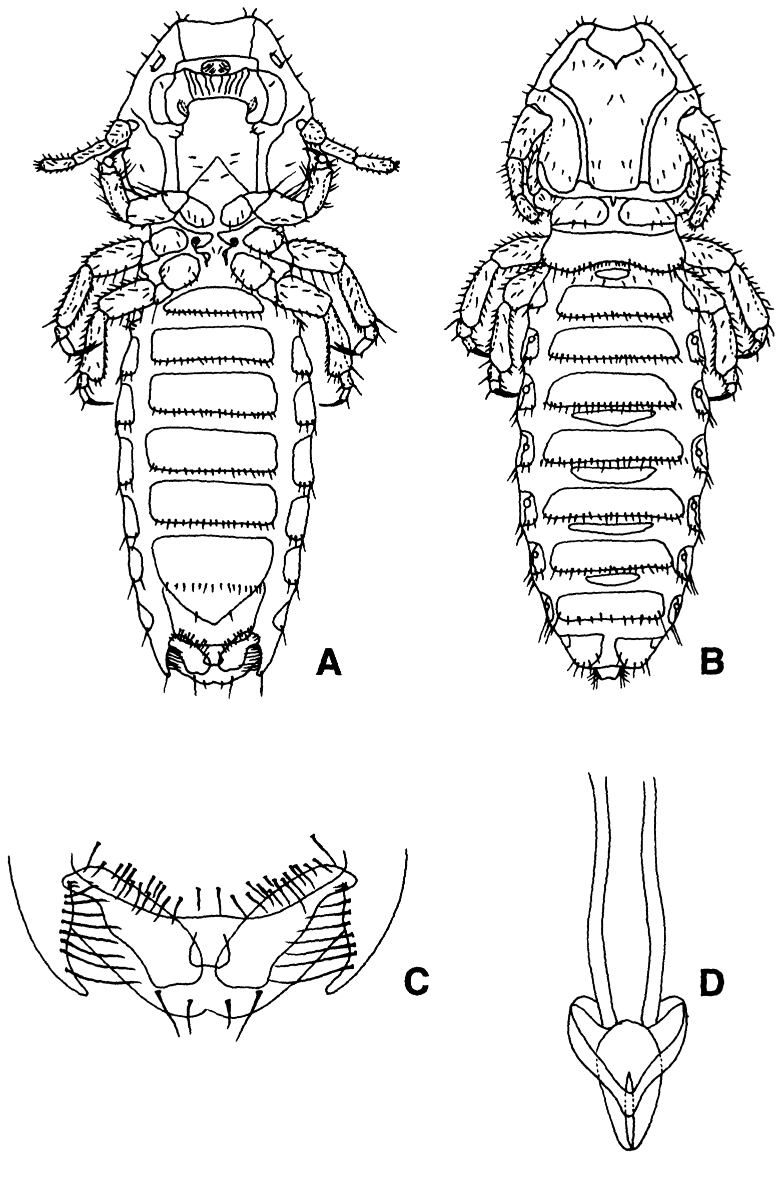


Figure 84. *Tricholipeurus parallelus*: ***A***, Ventral view of female; ***B***, dorsal view of male; ***C***, female terminalia; ***D***, male genitalia. Redrawn with minor modification by Jan Read from Emerson and Price (1975); courtesy of Brigham Young University Science Bulletin, Biological Series.

SUBORDER RHYNCHOPHTHIRINA[2]

Ferris (1931) erected the suborder to accommodate a single species, the elephant louse, that was obviously related to both Mallophaga and Anoplura but that differed from both in several important ways. The elephant louse had been discovered by Edouard Piaget, who collected specimens from African elephants in the Rotterdam (Netherlands) Zoological Garden in 1869 and described a new genus and species, *Haematomyzus elephantis* (Piaget 1869). Since he considered it to be a sucking louse, a very reasonable assumption for a louse with a long proboscis (fig. 85), Piaget placed his new species in Anoplura. At least in part due to its rarity, the elephant louse was little studied for over half a century, and Piaget's placement was accepted as correct until G.F. Ferris compared it with other chewing and sucking lice and found that the proboscis is not a piercing organ but has chewing mouthparts at its apex. Consequently, he moved *H. elephantis* to Mallophaga but, because it was so unlike Amblycera and Ischnocera, placed it in a new suborder, Rhynchophthirina. The family Haematomyzidae, which Enderlein (1904) had established in Anoplura for the elephant louse, was recognized by Ferris as the only family in the new suborder.

FAMILY HAEMATOMYZIDAE

Since Rhynchophthirina still contains only one family and one genus, descriptions of the suborder, family, and genus are the same.

Genus *Haematomyzus*

Lice of the genus *Haematomyzus* have a prognathous head that is roughly triangular with the posterolateral margins rounded and bearing a long, slender rostrum often referred to as a proboscis (fig. 85). The proboscis is longer than the remainder of the head and is not of the piercing type. The most conspicuous parts of the relatively small chewing mouthparts, which are attached to the apex of the proboscis, are the mandibles with their outward facing teeth (fig. 86). The five-segmented antennae are attached to the head posterior to the base of the proboscis and differ from other Mallophaga and from Anoplura by having a basal joint almost as long as the next three joints (fig. 87). The fourth and fifth joints lack the sensory pits that are found in Anoplura (Mukerji and Sen-Sarma 1955).

The thorax is short and broad and lacks dorsal sutures to divide it into segments. The apparent segment—the true mesothorax and metathorax—is the pterothorax (Emerson and Price 1988). A single pair of thoracic spiracles is located ventrally but near the lateral margins of the thorax. The legs are long and slender and terminate in a single stout claw (fig. 88). In shape of the thorax and morphology of the legs, *Haematomyzus* differs from anything in Anoplura and the other Mallophaga.

The abdomen of both sexes is broadly oval and is divided into eight visible segments that are easily recognizable. The true first segment is suppressed, and the first apparent segment is morphologically the second segment. The dorsal surface of females is marked with tergites that on the first (apparent) segment through the sixth are divided into narrow middorsal tergites and large lateral tergites. The seventh apparent segment is covered with a broad dorsal plate, presumably formed by a fusion of the lateral and middorsal tergites. In males, all tergites are fused. Abdominal spiracles are present on the third (second apparent) to the eighth segments near the lateral margins of the dorsum.

The genital apparatus is located on the seventh (apparent) abdominal segment (Mukerji and Sen-Sarma 1955). The most conspicuous part of the female external genitalia are the gonopophyses (fig. 89) (Weber 1938a). The male genitalia consist of an extrusible bulb attached to a median basal plate with parameres on the sides. The tips of the parameres are sharply curved upward (fig. 90). Jeu et al. (1990) studied the morphology of *H. elephantis* with the scanning electron microscope.

The genus now contains three species. Emerson and Price (1988) included a key to the species of *Haematomyzus* with their description of the third species. The fact that two of the species are found only in Africa weakly supports the idea that the ancestral *Haematomyzus* was African.

Haematomyzus elephantis

The elephant louse, as *Haematomyzus elephantis* has been known from the time it was first described, is a parasite of the Asiatic elephant (*Elephas maximus*) and the African elephant (*Loxodonta africana*). The louse has been collected from elephants that had been in long-time captivity and from wild elephants—that is, from recently captured Asiatic elephants and from captive elephants in widely scattered parts of Asia. It appears that its distribution approximates that of its hosts. Clay (1963) speculated that the louse evolved on one of the elephants and transferred to the other, but could not find evidence to support her hypothesis.

Information about the life history and economic importance of *H. elephantis* is fragmentary. This louse inhab-

[2]From Gk. *rhynchos* a beak, snout; Gk. *phthir* a louse. Ferris (1931) proposed Rhyncophthirina for his new suborder but, based on the Greek spelling of *rhynchos*, the name should be spelled Rhynchophthirina.

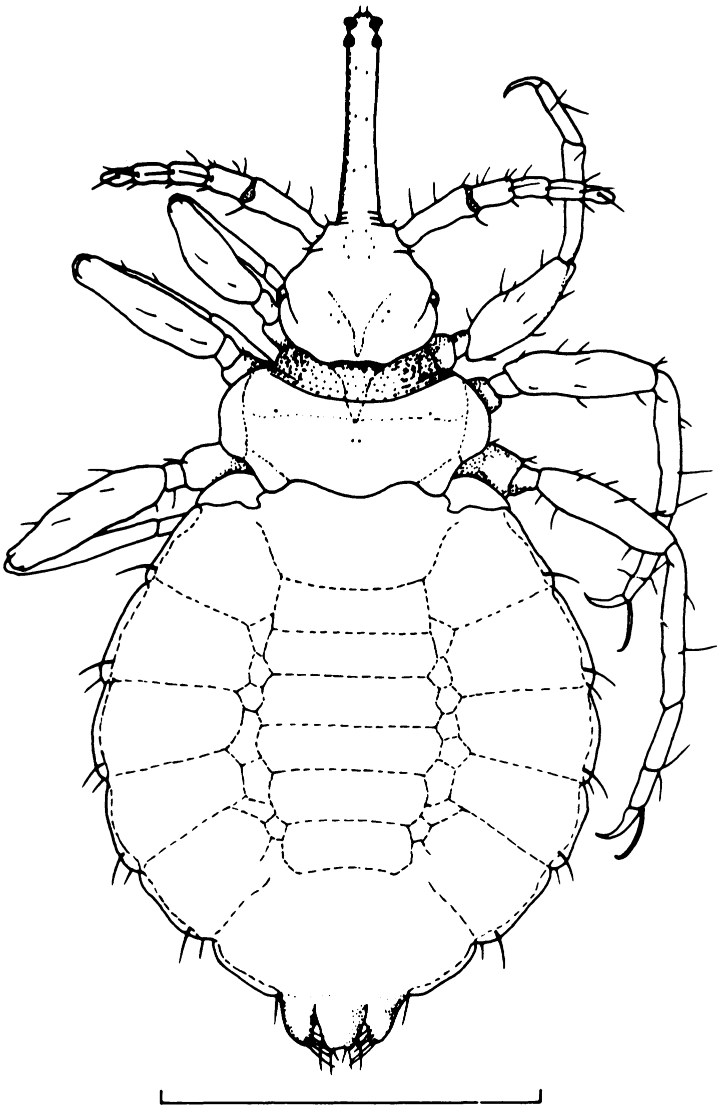


Figure 85. *Haematomyzus elephantis* (elephant louse): Dorsal view of female. From Marshall (1981), reprinted by permission of Academic Press Ltd, London.

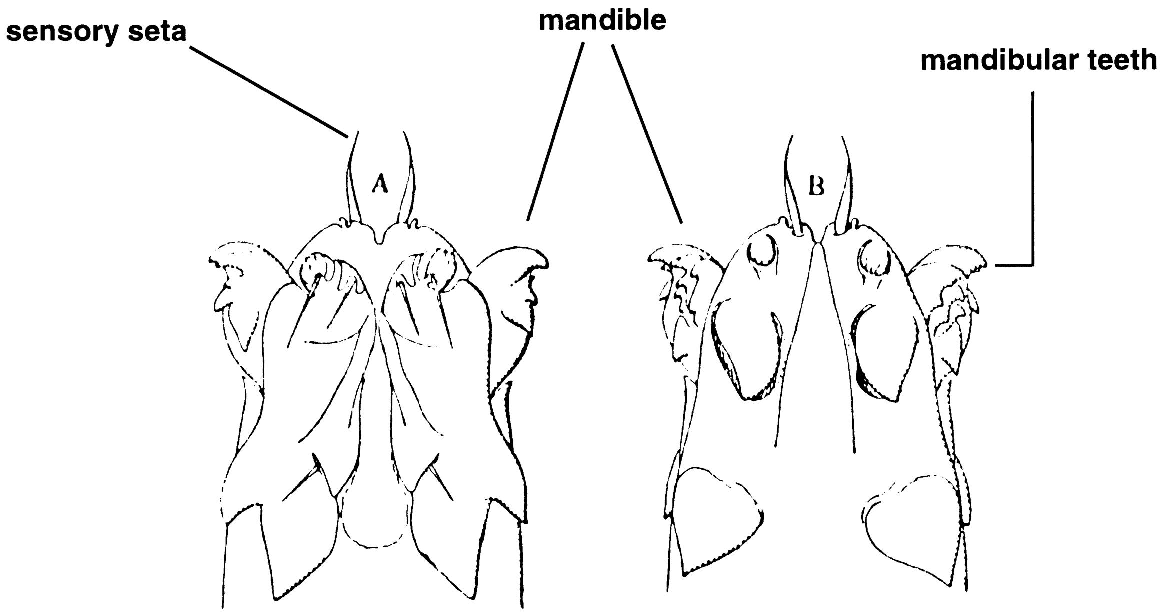


Figure 86. Structural details of *Haematomyzus elephantis*: ***A***, Ventral view of apex of proboscis; ***B***, dorsal view of same. From Ferris (1931), reprinted by permission of Cambridge University Press.

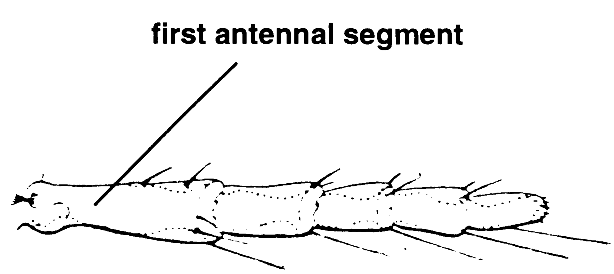


Figure 87. *Haematomyzus elephantis*: Antenna with its long first segment. From Ferris (1931), reprinted by permission of Cambridge University Press.

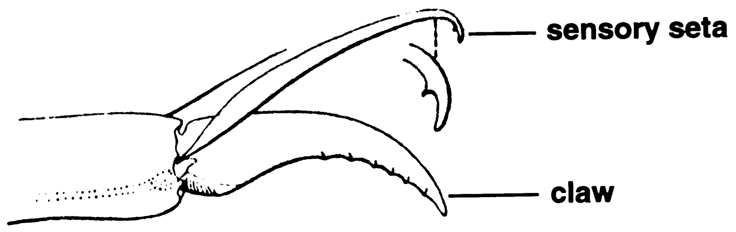


Figure 88. *Haematomyzus elephantis*: Apex of tarsus with its single well-developed claw and poorly understood sensory seta. From Ferris (1931), reprinted by permission of Cambridge University Press.

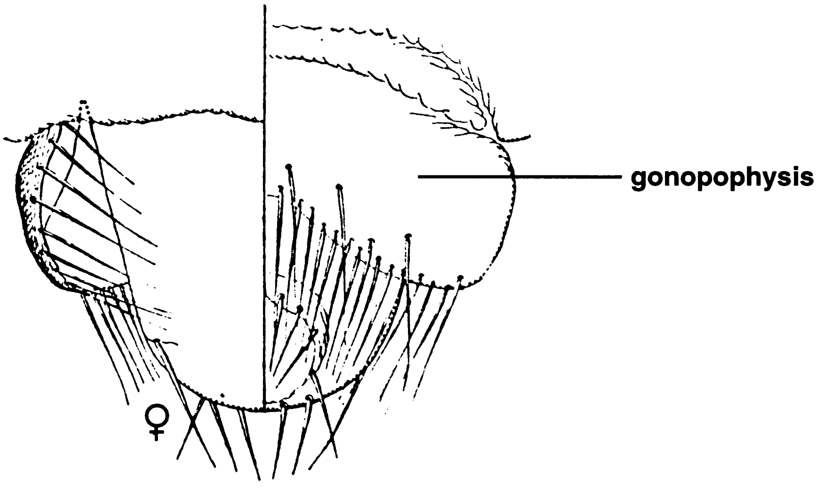


Figure 89. *Haematomyzus elephantis*: Dorsoventral view of female terminalia. From Ferris (1931), reprinted by permission of Cambridge University Press.

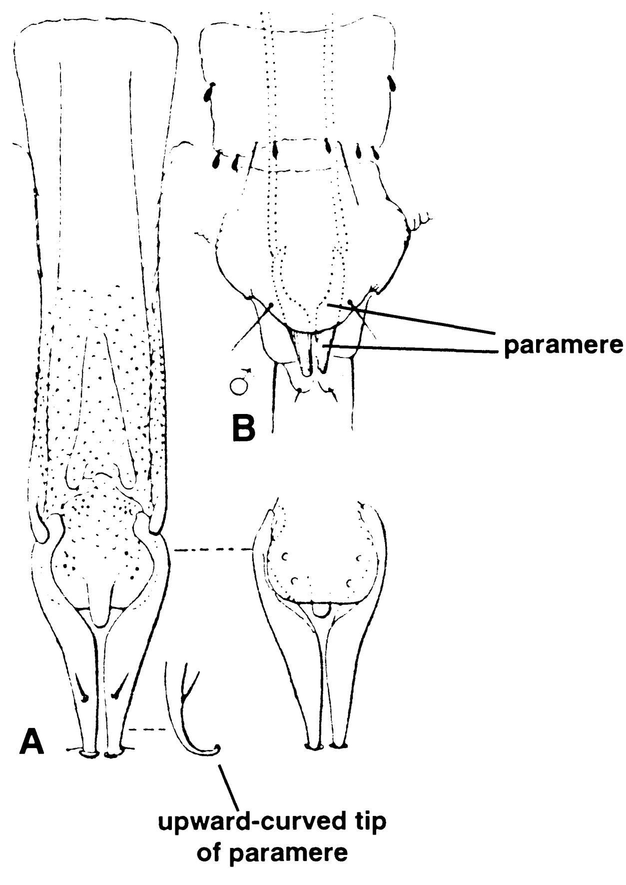


Figure 90. Male *Haematomyzus elephantis*: ***A***, Genitalia (note that tips of parameres curve upward sharply); ***B***, ventral view of tip of abdomen showing the relation of genitalia to abdominal segments. From Ferris (1931), reprinted by permission of Cambridge University Press.

its folds in the skin of the ear, axillae, groin, and root of the tail of the host. It is common on the hairy ears of young elephants (Emerson and Price 1985). It differs from other Mallophaga and all Anoplura in that the louse attaches itself to the host by anchoring the highly modified rostrum in the host tissues (Baker and Chandrapatya 1992). Mukerji and Sen-Sarma (1955) mentioned that lice are seldom seen on well-groomed animals. Eggs of *H. elephantis* are similar to those of Anoplura and of other Mallophaga (Ferris 1931) (fig. 91) but are distinctive. Anatomically the proboscis is capable of sucking fluids but—despite the statement by Mukerji and Sen-Sarma that the proboscis is used to ingest a blood meal—the exact nature of the elephant louse's food is not known. Hopkins (1957) conjectured that skin secretions and skin debris are used as food.

Three elephants at the Nehru Zoological Park, Hyberdad, India, were found to be infested with *H. elephantis*; one was so severely infested that it required an insecticidal treatment (Raghavan et al. 1968). These authors also mentioned that many lice were so firmly attached that the proboscis of each was broken when the lice were collected.

Haematomyzus hopkinsi

For years, collections of *Haematomyzus* sp. from wart hogs in Kenya and Uganda were assumed to be *H. elephantis*, but Clay (1963) found that they were a new species, which she described as *Haematomyzus hopkinsi*. The new species has a shorter proboscis than that in *H. elephantis*, and males have four clear, circular areas with a prominent seta in the center of each along each side of the abdominal dorsum. Females differ from females of *H. elephantis* in the shape of the posterior margin of the abdomen.

The life history of *H. hopkinsi* has not been reported. Its populations on its host are apparently higher than those of *H. elephantis* (Hoogstraal 1958).

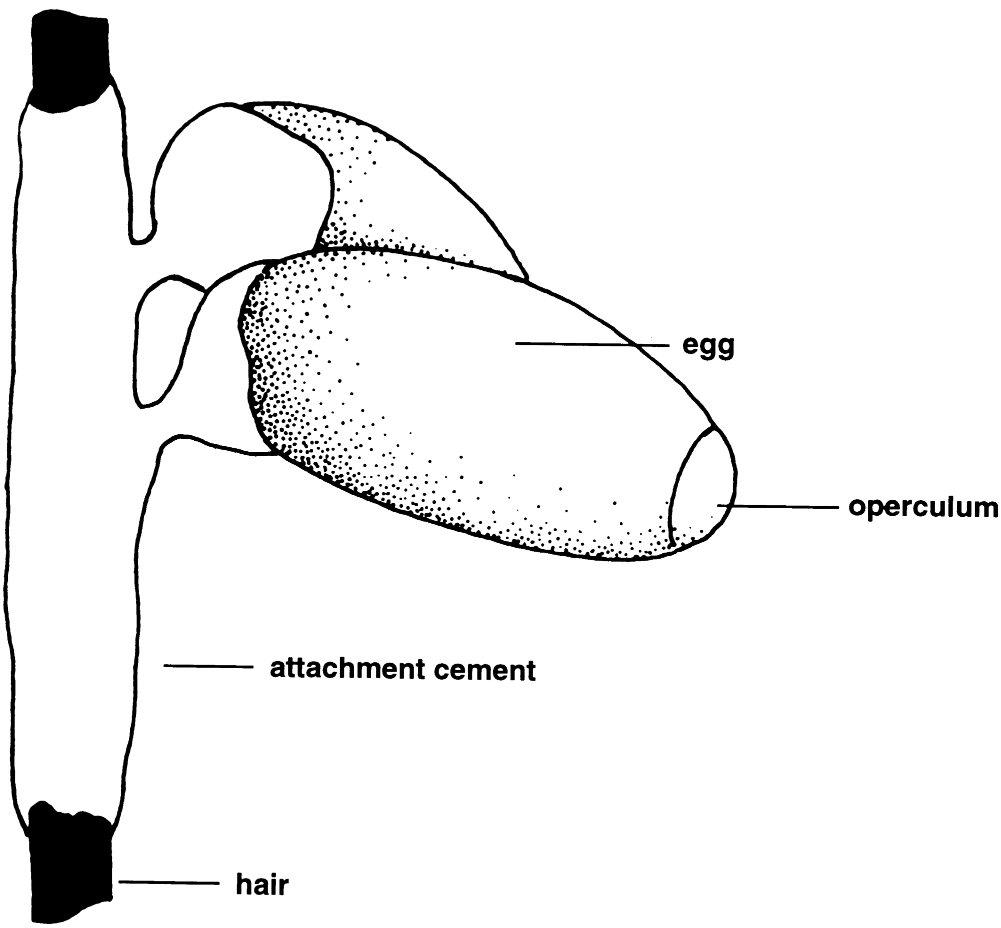


Figure 91. Egg of *Haematomyzus elephantis*. From Marshall (1981), reprinted by permission of Academic Press Ltd, United Kingdom.

Haematomyzus porci

In 1988 Emerson and Price described a third species as *Haematomyzus porci*. This louse infests the bush pig (*Potamochoerus porcus*) in Ethiopia. The host is found on Madagascar as well as on the African mainland, but *H. porci* is known only from the type location.

H. porci closely resembles the other two species in the genus and, like *H. hopkinsi*, has a shorter proboscis than does *H. elephantis*. Male *H. porci* have five pair of clear, circular areas on the abdomen. Females have a pterothorax not as wide as that of *H. hopkinsi*. The life history is not yet known.

ORDER ANOPLURA (SUCKING LICE)

The name Anoplura was first proposed by Leach (1815) for both the sucking and chewing lice and was later revived by von Dalla-Torre (1908) for sucking lice alone (Ferris 1951). Piaget (1880) avoided the use of an ordinal name for sucking lice; instead he placed them in a single family, the Pediculidae, with six genera.

All members of the order Anoplura are wingless insects that are flattened dorsoventrally. The head is narrower than the prothorax and contains piercing-sucking mouthparts in a trophic sac within the head capsule. The mandibles are usually absent or at most rudimentary. The tentorium is absent (Symmons 1952, Kim and Ludwig 1982). The thorax is unsegmented, and the single pair of mesothoracic spiracles are located dorsally (fig. 92). The Anoplura have a one-segmented tarsus with a single claw and no pulvillus. The abdomen usually has six pair of spiracles that open on abdominal segments 3–8 but occasionally has fewer (Kim 1985). Keys to the North American Anoplura have been prepared by Stojanovich and Pratt (1965) and by Kim et al. (1986).

All of the approximately 500 species of sucking lice are parasites of mammals. Lehane (1991) calculated that two-thirds of all Anoplura are parasites of rodents. Sucking lice inhabit the skin-fur environment of their hosts, the dermecos of Moreby (1978), where they feed exclusively on blood (Kim 1985). Heavy infestations of sucking lice may cause severe debilitation, anemia, and weakness of the host (Sosna and Medleau 1992a).

Anoplura are found on eutherian mammals of all classes except Chiroptera (bats), Edentata (sloths, armadillos), Marsupialia (marsupials), Cetacea (whales), Proboscidea (elephants), and Sirenia (manatees). Body size varies from 0.35 mm long in *Microphthirus* to more than 8 mm long in *Pecaroecus.* Although there are no fossil records of Anoplura, it is believed that they are a monophyletic group that made a major change in their feeding habits when they began to ingest blood during the late Cretaceous or early Paleocene time periods (Kim and Ludwig 1982). Anoplura must have existed in the mid-Cretaceous period (Hopkins 1949). A phylogeny of the Anoplura was constructed by Kim and Ludwig (1978a), which they based on a study of the evolution of the mammalian hosts (fig. 93).

For many years, workers with Anoplura followed Ferris (1951), who placed the then-known 255 species of sucking lice in 6 families while recognizing 5 subfamilies of Hoplopleuridae. The number of species increased to 493 (Kim 1988) and then to 532 (Durden and Musser 1994a). The number of families recognized by Kim and Ludwig (1978a), who elevated all of Ferris' subfamilies to family rank, was 15. Kim and Ludwig's classification is compared with Ferris' in table 7. It is noted that 10 families listed by Kim and Ludwig contain only 1 genus (Marshall 1981), and some have only 1 species.

The geographic distribution of the Anoplura is cosmopolitan, but they are far from evenly distributed among the zoogeographical regions of the world. Ludwig (1968) recorded 135 species, 34% of the sucking lice then known, from the Ethiopian Region. At the other extreme, in the Australian Region most of the few species were introduced with their hosts; only six species of *Hoplopleura* are indigenous to the region (Calaby 1970).

FAMILY ECHINOPHTHIRIIDAE

All of the medium-to-large lice in the family Echinophthiriidae are parasites of aquatic carnivores: seals, walruses, and sea lions (Pinnipedia) or river otters (Mustelidae). Their head and thorax are thickly covered with conspicuous setae that may be modified to spiniform setae (fig. 94). The eyes are not evident externally. The thorax does not have a sternal plate; the sternal apophyses and apophyseal pits are indistinct. The thoracic phragmata are well developed. The forelegs are small and slender and taper to a sharp point, except in *Echinophthirius* where the forelegs are equal to the midlegs. The abdomen is leathery and membranous and usually thickly covered with setae that may be modified into pegs or scales. The six pairs of abdominal spiracles are small, and each has a long, slender atrial chamber with a sophisticated closing device (Kim and Emerson 1974). The spermathecae are absent. The gonopods on segment 8 of the female never form free lobes. The vagina is surounded by thick patches of long setae (Kim and Ludwig 1978b). Males, females, and the three nymphal instars of *Echinophthirius horridus* were described by Beder (1990); measurements and scanning electron micrographs were included in the publication.

As established by Enderlein (1904), the Echinophthiriidae consisted of two genera: *Echinophthirius* by original designation and *Lepidophthirus* (fig. 95) by original description. To these two, Enderlein (1906) added *Antarctophthirus* with its six species, Ewing (1923) added *Proechinophthirus* with two species, and Kim and Emerson (1974) added the monotypic *Latagophthirus*, a parasite of a river otter, *Lutra canadensis* (Carnivora: Mustelidae). The 12 species of Echinophthiriidae and their hosts are listed in appendix B. Stojanovich and Pratt (1965) provided a key to the five species of North American Echinophthiriidae known at that time.

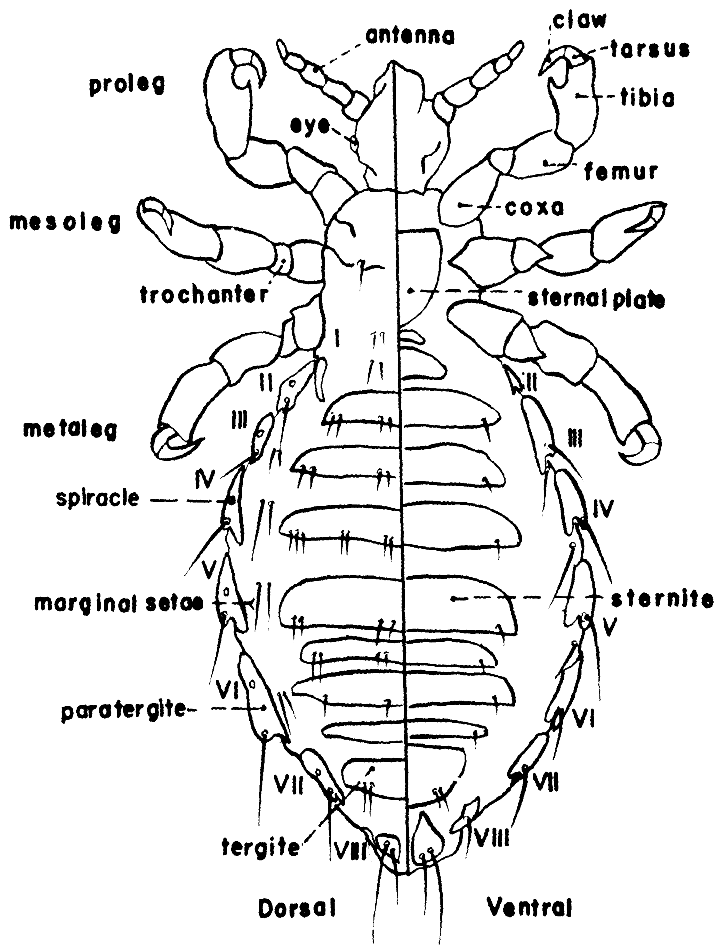


Figure 92. Generalized drawing of an anopluran, with body parts labeled. From Ignoffo (1959), reprinted by permission of American Midland Naturalist.

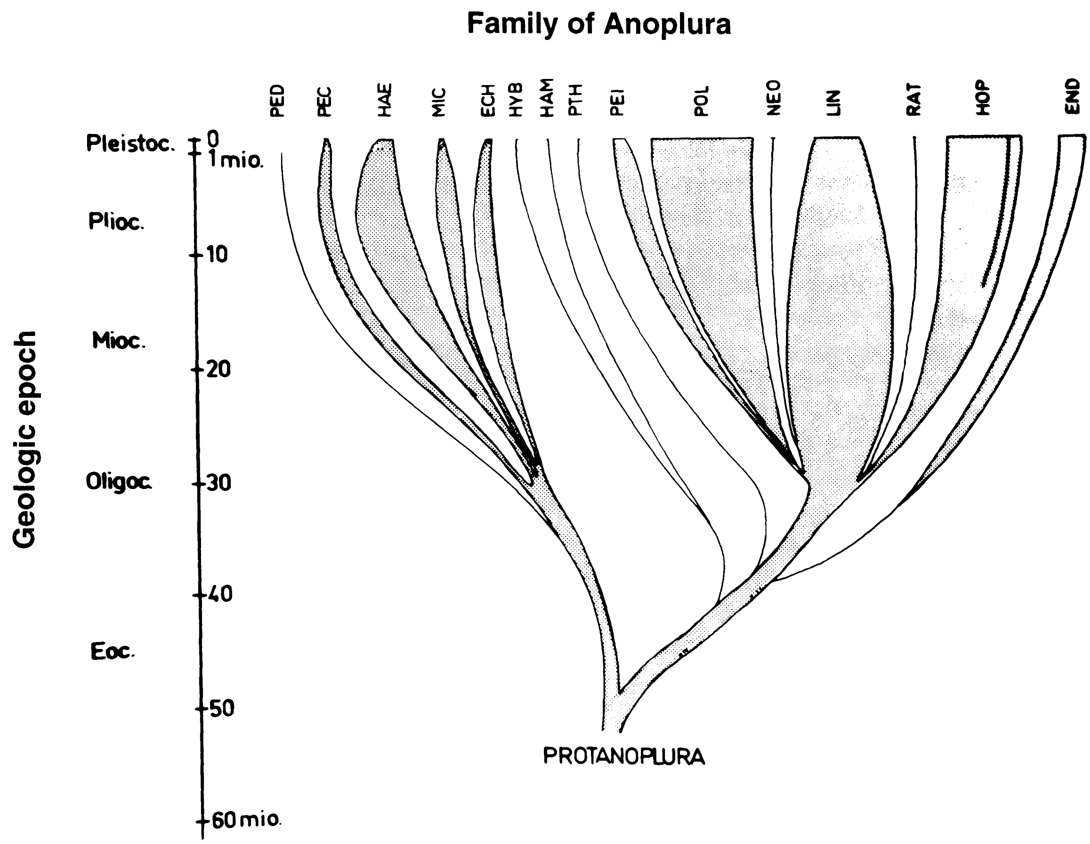


Figure 93. Inferred phylogeny of Anoplura. From Kim and Ludwig (1978a), reprinted by permission of Blackwell Science Ltd, Oxford, United Kingdom.

Table 7. Comparison of two systems of classification of Anoplura

System of Ferris (1951)	System of Kim and Ludwig (1978)
Echinophthiriidae	Echinophthiriidae
Linognathidae (*Linognathus, Solenopotes, Prolinognathus,* **Microthoracius*)	Linognathidae Microthoraciidae; new family
Haematopinidae (Haematopinus, *Pecaroecus)	Haematopinidae Pecaroecidae
Hopopleuridae	
*Subfamily Enderleinellinae	Enderleinellidae
Subfamily Hoplopleurinae (*Hoplopleura, Pterophthirus, Schizophthirus, Ancistroplax, Haematopinoides*)	Hoplopleuridae Subfamily Hoplopleurinae Subfamily Haematopinoidinae (*Schizophthirus, Ancistroplax, Haematopinoides*)
Subfamily Polyplacinae (*Polyplax* and other genera, **Hamophthirius,* **Ratemia*)	Polyplacidae Hamophthiriidae Ratemiidae, new family
*Subfamily Hybophthirinae	Hybophthiridae
*Subfamily Pedicininae	Pedicinidae
Neolinognathidae	Neolinognathidae
Pediculidae (*Pediculus,* **Pthirus*)	Pediculidae Pthiridae

* Asterisk indicates a taxon whose taxonomic status was changed by Kim and Ludwig (1978a).

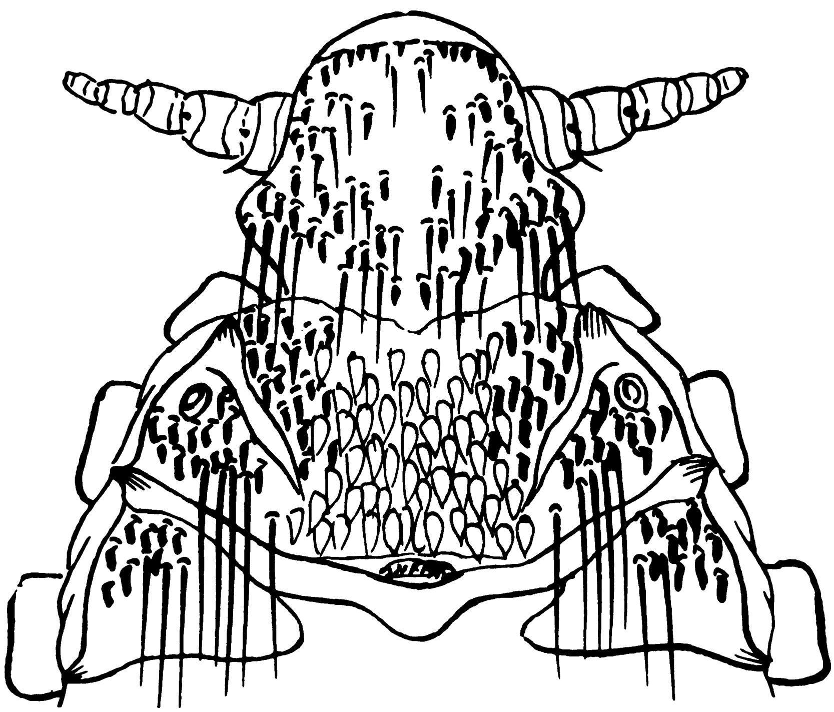


Figure 94. Family Echinophthiriidae: Head and thorax thickly covered with setae and modified setae. From Stojanovich and Pratt (1965), Key to Anoplura of North America, U.S. Department of Health, Education, and Welfare.

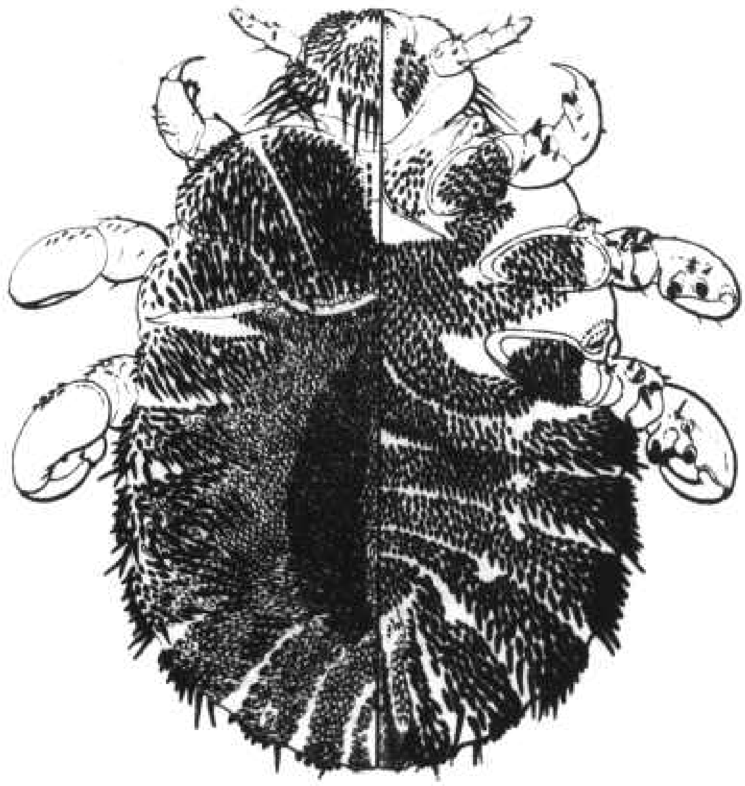


Figure 95. *Lepidophthirus macrorhini*: Dorsoventral view of female. From Ferris (1951), reprinted by permission of Pacific Coast Entomological Society.

Seals and other marine carnivores that are hosts for Echinophthiriidae may swim out in the ocean as far as 5,000 mi in winter, but in summer they go ashore to their rookeries where their young are born. Lice apparently transfer rapidly from the cows to their pups, and all or most of the louse reproduction occurs on the pups while they are in the rookeries.

Only two entomologists, M.D. Murray in Australia and K.C. Kim in the United States, have attempted to study the life history of these unusual parasites. The next paragraph contains a composite life history of two species of Echinophthiriidae: *Antarctophthirus callorhini* from the northern fur seal (*Callorhinus ursinus*) and *Antarctophthirus ogmorhini* from the Weddell seal (*Leptonychotes weddelli*). Our information is taken from Murray et al. (1965), Kim (1971, 1972, 1975), and Kim et al. (1975).

Antarctophthirus ogmorhini are adults when the Weddell seal "hauls out" on the icy beaches of Antarctica, whereas *Antarctophthirus callorhini* are second-instar nymphs when its host, the northern fur seal, goes ashore (a few first-instar nymphs may be present). Both forms of the louse leave the mother seal and go to the newborn pup in large numbers, perhaps because the skin temperature of the pup is about 6 °C higher than that of the cow. Also, the fur of the pup is much thinner and easier for the louse to penetrate. Both louse species take a blood meal quickly; *A. ogmorhini* engorges in 23 min at temperatures of 10–20 °C and *A. callorhini* in less than 10 min. Within 3–4 days, *A. callorhini* leaves the belly of the pup and goes to the naked parts of the body: the nostrils, eyelids, auditory canal, penile opening, and umbilical area. *A. ogmorhini* is most apt to select the hind flippers, tail, ankle, and hip. Apparently all stages of the louse prefer those areas that may be warmer than the body as a whole. *A. callorhini* was densely aggregated around the penile orifice and anal area on the fourth and fifth day after the pup was born; some were in the auditory canal by the sixth day and in the nostrils and on the eyelids by the seventh or eighth day.

For *A. callorhini*, the first-instar nymphs molt after 2–3 days and the second- and third-instar nymphs after 4 days at an ambient temperature of 11–15 °C and a host skin temperature of 31 °C. Females have two ovaries and five oviducts in each ovary; they oviposit at the rate of 8–10 eggs/day. A life cycle is completed in approximately 18 days. It was estimated that the louse completes four generations while on land and a fifth generation at sea, but about 8 mo is required for that last generation. For *A. ogmorhini*, it was estimated that a life cycle was completed in 3–4 wk. Eggs were often placed on the hind flippers. It appears that the optimum temperature for *A. ogmorhini* is 5–15 °C.

FAMILY ENDERLEINELLIDAE

Members of the family Enderleinellidae are the smallest of all Anoplura; some are no longer than 0.35 mm. They do not have a postantennal projection. The thoracic phragmata are poorly developed. The sternal plate is usually well developed; if it is weakly developed or absent, the coxae are widely separated. The forelegs are only slightly smaller than the midlegs; compared with the hindlegs, both are small and slender. Each foreleg and midleg has a slender claw. The hindlegs are stout, with a hind tibiatarsus that is well developed and terminates in a large, stout claw. The sternal and tergal plates of the abdominal segments are either poorly developed or absent (Kim et al. 1986).

The Enderleinellidae parasitize squirrels (mammalian family Sciuridae). They are found worldwide except in Australia and a few small, isolated regions. The family contains 5 genera and 50 species (see appendix B) (Kim et al. 1990). A key to the genera can be found in Kim (1977). The species most likely to be encountered by squirrel hunters in the United States are *Enderleinellus kelloggi* from western gray squirrels, *E. longiceps* from fox squirrels and eastern gray squirrels, and *E. tamiascuri* from red squirrels and Douglas' squirrels (Kim et al. 1986).

FAMILY HAEMATOPINIDAE

When Enderlein established Haematopinidae in 1904, it was a large family in which he placed all of the Anoplura except the body louse of humans (Pediculidae), the elephant louse (Haematomyzidae), and the lice of marine carnivores (Echinophthiriidae). Ewing (1929) followed this system of classification but separated Haematopinoididae (from moles) and Pthiridae (crab louse of humans) from Haematopinidae and established them as new families. Five subfamilies and 33 genera of sucking lice remained in Haematopinidae after this separation. Ferris (1951) recognized only two genera of Haematopinidae: the type genus and, doubtfully, *Pecaroecus* (from the peccary). Modern taxonomists (Kim and Ludwig 1978b, Kim et al. 1986) have placed *Pecaroecus* in its own monotypic family, thus leaving *Haematopinus* with approximately 20 species as the only genus of Haematopinidae (Kim 1988, Kim et al. 1990).

The family was described by Kim and Ludwig (1978b) as medium-to-large sucking lice without external evidence of eyes but with prominent ocular points (fig. 96) posterior to five-segmented antennae. The thorax has a distinct notal pit and a mesothoracic phragma that continues across the dorsum to enclose the notal pit. The thoracic sternal plate is well developed. Three pair of legs are subequal in size and shape, and each has a distotibial process (figs. 97, 98). The abdomen has

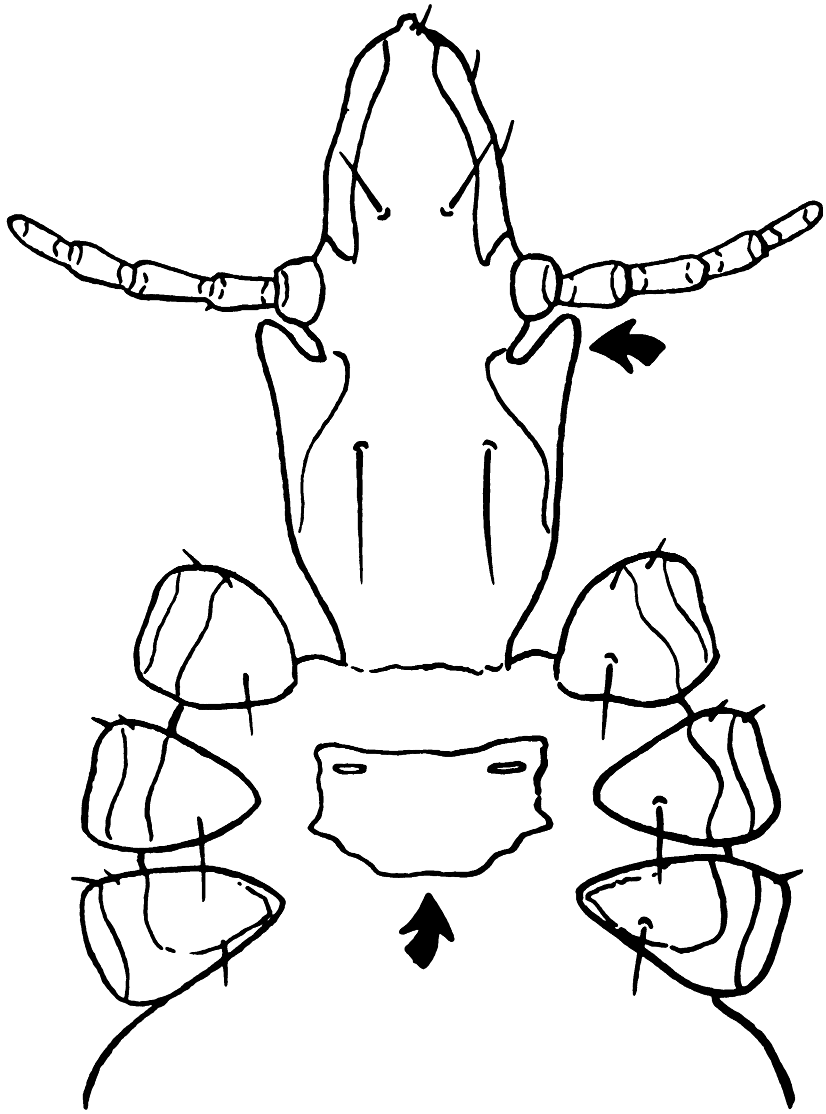


Figure 96. Characteristics of *Haematopinus* spp. Prominent ocular point (top arrow); note shape of sternal plate (bottom arrow). From Stojanovich and Pratt (1965), Key to Anoplura of North America, U.S. Department of Health, Education, and Welfare.

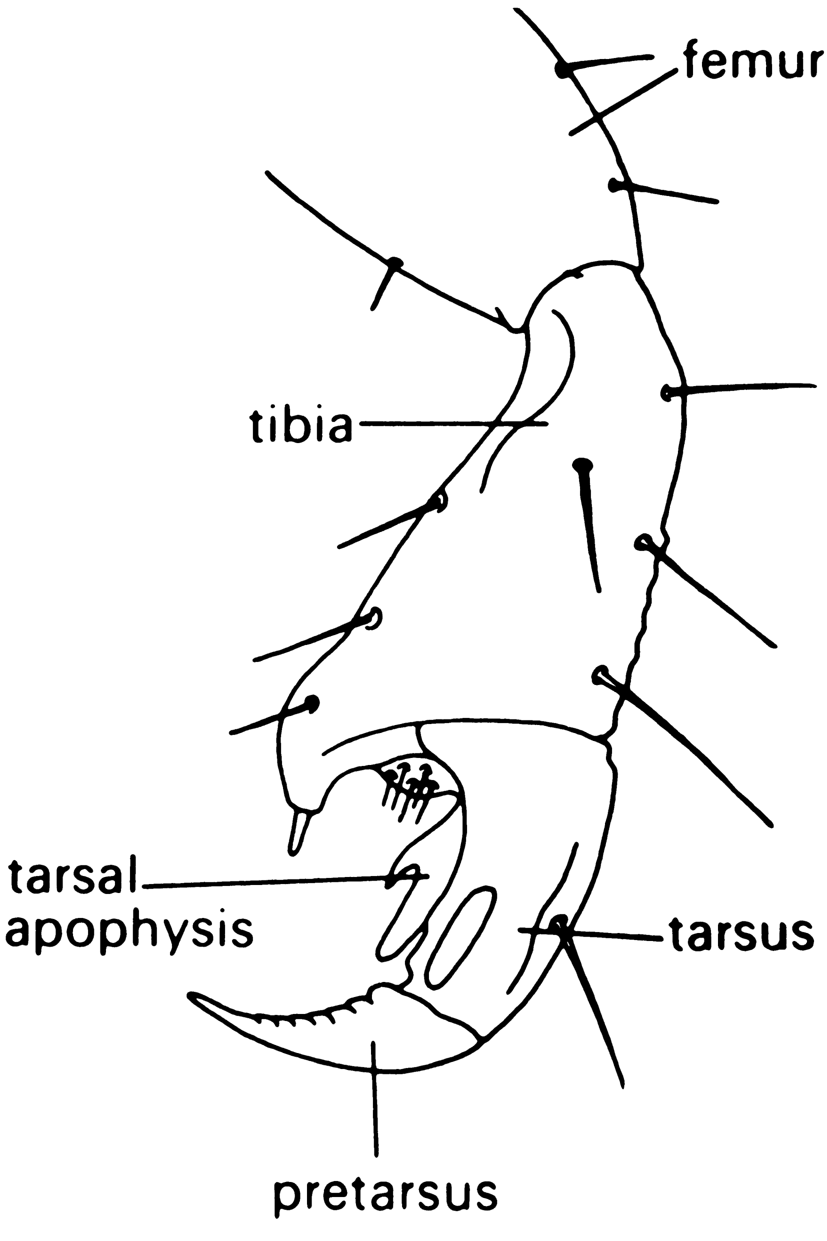


Figure 97. Apex of leg of *Haematopinus* sp. Reprinted with permission from Chapman (1982), The Insects: Structure and Function, 3d ed., Harvard University Press, Cambridge, Massachusetts.

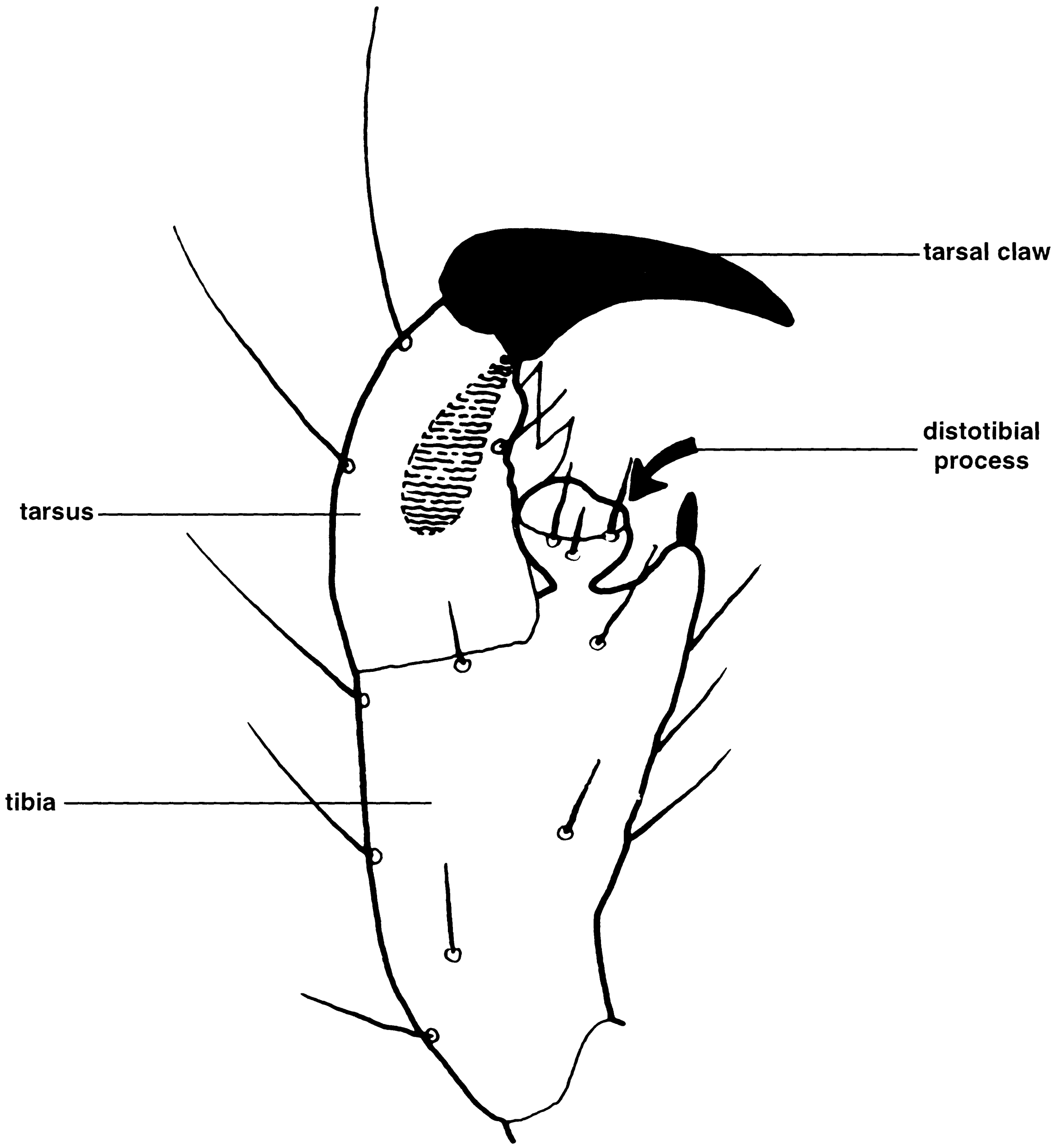


Figure 98. Apex of *Haematopinus* leg. From Kim and Ludwig (1978a), reprinted by permission of Blackwell Science Ltd, Oxford, United Kingdom.

strongly sclerotized caplike paratergites on prominent lateral lobes on segment 2 or 3 to 8. Male and female genitalia are as shown in figures 99 and 100.

Genus *Haematopinus*

As the only genus in the family Haematopinidae, *Haematopinus* has the characteristics described above. The haematopinids parasitize Artiodactyla (Suidae, Bovidae, and some Cervidae) and Perissodactyla (Equidae). Two records of *Haematopinus* from Camelidae are erroneous because they were taken fron contaminated collections (Kim and Ludwig 1978b). Durden (1991b) listed new records for five species of *Haematopinus* fron native African ungulates (see appendix B), and Horak et al. (1991a) recovered *H. latus* from the bushpig (*Potamochoerus porcus*).

Haematopinus asini (horse sucking louse)

As shown in figure 101, *Haematopinus asini* has a long, narrow, pointed head that is longer than the thorax and 2–2.5 times as long as it is broad. The ocular points, also called postantennal angles, are prominent. The basal portion of the head is constricted where it joins the thorax. The thorax has a rectangular sternal plate that is only slightly longer than broad and does not have a median projection. The legs are short and stout and have a small pretarsal sclerite (= distotibial process) (fig. 102). The small elliptical abdomen has a pair of conical paratergal plates on each of apparent segments 2–7. The female is about 3 mm long and the male 2.25 mm long (Kim et al. 1986). The five subspecies of *H. asini* recognized by Webb (1948) have not been confirmed by subsequent workers.

The horse sucking louse has been carried to all parts of the world with its hosts. But it is most abundant in the temperate regions and is seldom seen in the tropics except in the cooler mountainous areas.

Life history. Female *H. asini* may deposit 50–100 eggs in a lifespan of 4–5 wk (Butler 1985). Although the incubation period may vary from 11 to 20 days, it is more likely to be 12–14 days (Schwartz et al. 1930). Under their conditions, Bacot and Linzell (1919) found that at 38 °C the eggs hatched in 15–17 days, but at a fluctuating temperature of 30–38 °C the maximum incubation period was extended to as many as 34 days. After the eggs hatch, another 11–12 days are required for nymphal development (Price et al. 1967b). In the United States, the lice are more abundant in winter than in summer (Loomis et al. 1975b). The horse sucking louse seems to prefer to locate at the roots of the forelock and mane, around the base of the tail, and on the hair just above the hooves, but heavily infested horses may have the lice on any part of the body (Roberts 1952). *H. asini* does not usually live more than 2–3 days off the host (Bishopp 1942).

Host-parasite relationships and economic importance. *Haematopinus asini* normally parasitizes horses, donkeys, and mules. It has also been reported from zebras in zoological gardens and from wild zebras in several areas of Africa (Stimie and van der Merwe 1968). It is spread from horse to horse by direct contact, and spread is more rapid if horses are in crowded quarters. The lice may also be spread by the shared use of curry combs, grooming brushes, saddle blankets, and other equipment.

Ewing (1929) stated that range horses are more susceptible to louse infestation than are stabled horses, and several writers have mentioned short rations and long, unkempt hair as favoring louse buildup. The untrained observer may not notice lice until the horses are heavily infested and are rubbing, scratching, and losing patches of hair. Continuous itching caused by the feeding of the lice makes the horses try to free themselves of lice, which results in bruises and lacerated skin. The growth of young colts that are heavily louse infested may be stunted. In addition, severe louse infestation may cause the horse to be anemic and thus be more susceptible to systemic disease (Bishopp 1942, Roberts 1952).

Haematopinus eurysternus (shortnosed cattle louse)

Of the *Haematopinus* of cattle, *H. eurysternus* is the smallest. The females average 2.88 mm long and the males 2.33. The head is short, nearly as broad as long, and is bluntly rounded at the apex (fig. 103). The front corners of the thoracic sternal plate are rounded, not elongated. The abdominal tracheal trunks are thin. The median subgenital plate is subtrapezoidal and is longer than wide. The ninth abdominal tergite has front corners that are elongated. The male subgenital plate has five to seven (usually six) anterior setae (Stojanovich and Pratt 1965, Stimie and van der Merwe 1968, Meleney and Kim 1974).

Early taxonomists confused *H. eurysternus* with *Solenopotes capillatus*. Nitzsch (1818) incorrectly described the little blue cattle louse as *Pediculus eurysternus*, and that name became a *nomen nudum*. The confusion of names for these two species of cattle lice ended only after the little blue cattle louse was described as *Solenopotes capillatus* by Enderlein in 1904 and after the International Commission on Zoological Nomenclature had conserved both *H. eurysternus* and *S. capillatus* (Kim and Weisser 1973, 1974).

In distribution, the shortnosed cattle louse is cosmopolitan but is more abundant in colder climates. In general, its distribution is the same as that of its principal host,

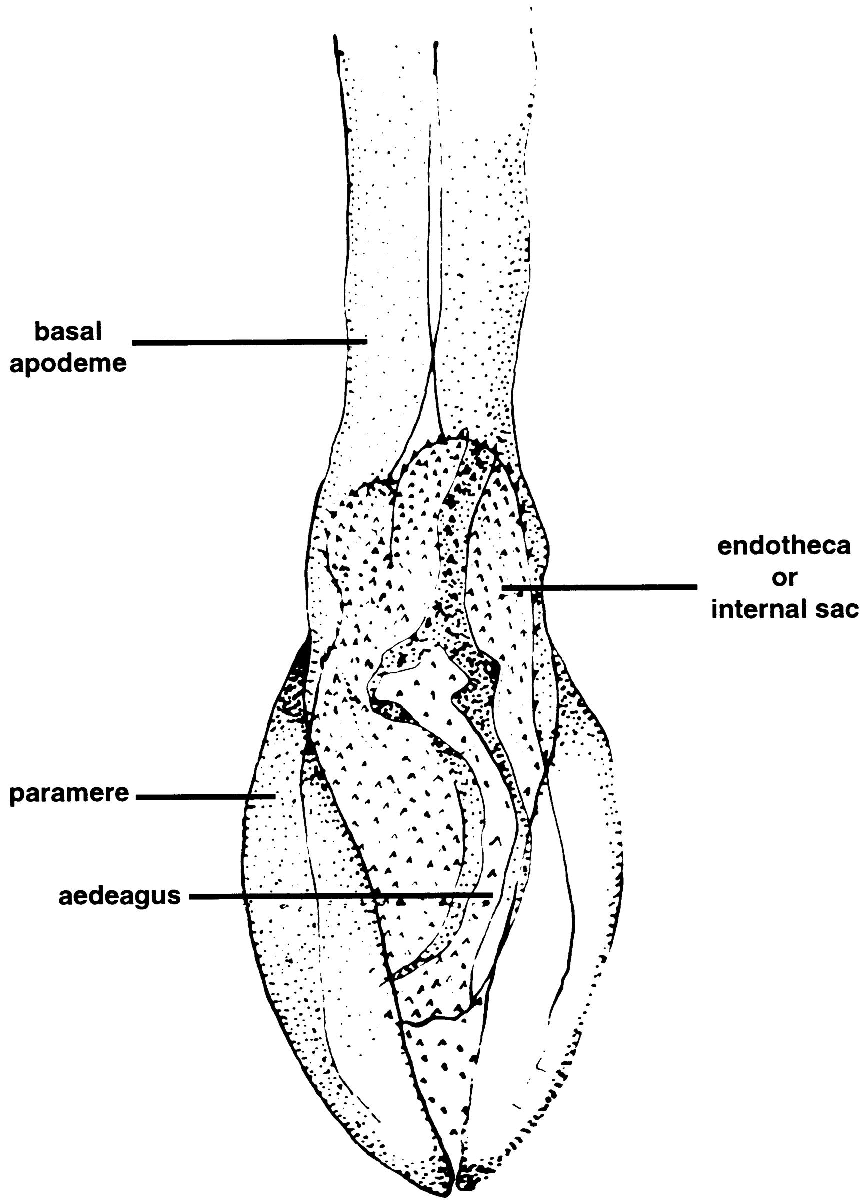


Figure 99. *Haematopinus apri*: Male genitalia. From Kim and Ludwig (1978a), reprinted by permission of Blackwell Science Ltd, Oxford, United Kingdom.

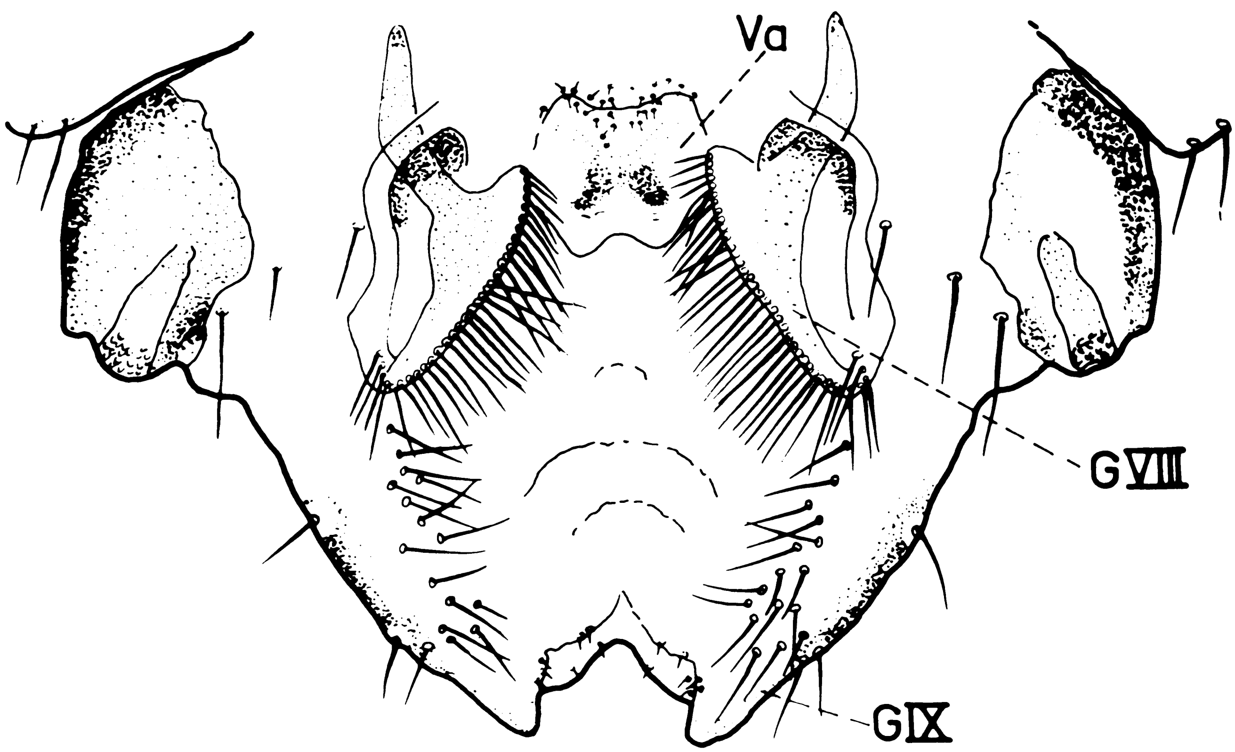


Figure 100. *Haematopinus taurotragi*: Female terminalia. Va = valvula, GVIII = gonopod (8th abdominal segment), GIX = gonopod (9th abdominal segment). From Kim and Ludwig (1978a), reprinted by permission of Blackwell Science Ltd, Oxford, United Kingdom.

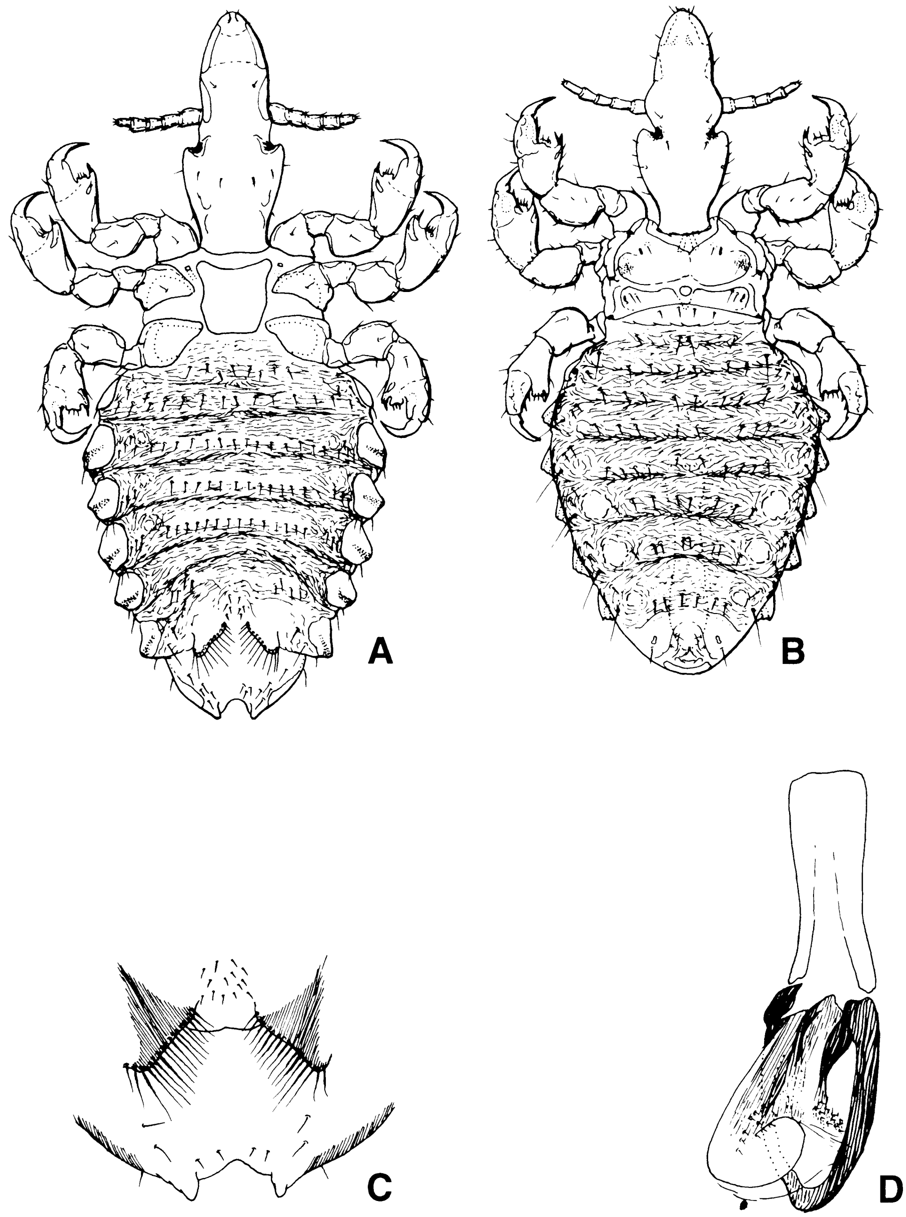


Figure 101. *Haematopinus asini* (horse sucking louse): ***A***, Ventral view of female; ***B***, dorsal view of male; ***C***, female terminalia; ***D***, male genitalia. Redrawn with minor modification by Jan Read from Ferris (1951); courtesy of Pacific Coast Entomological Society.

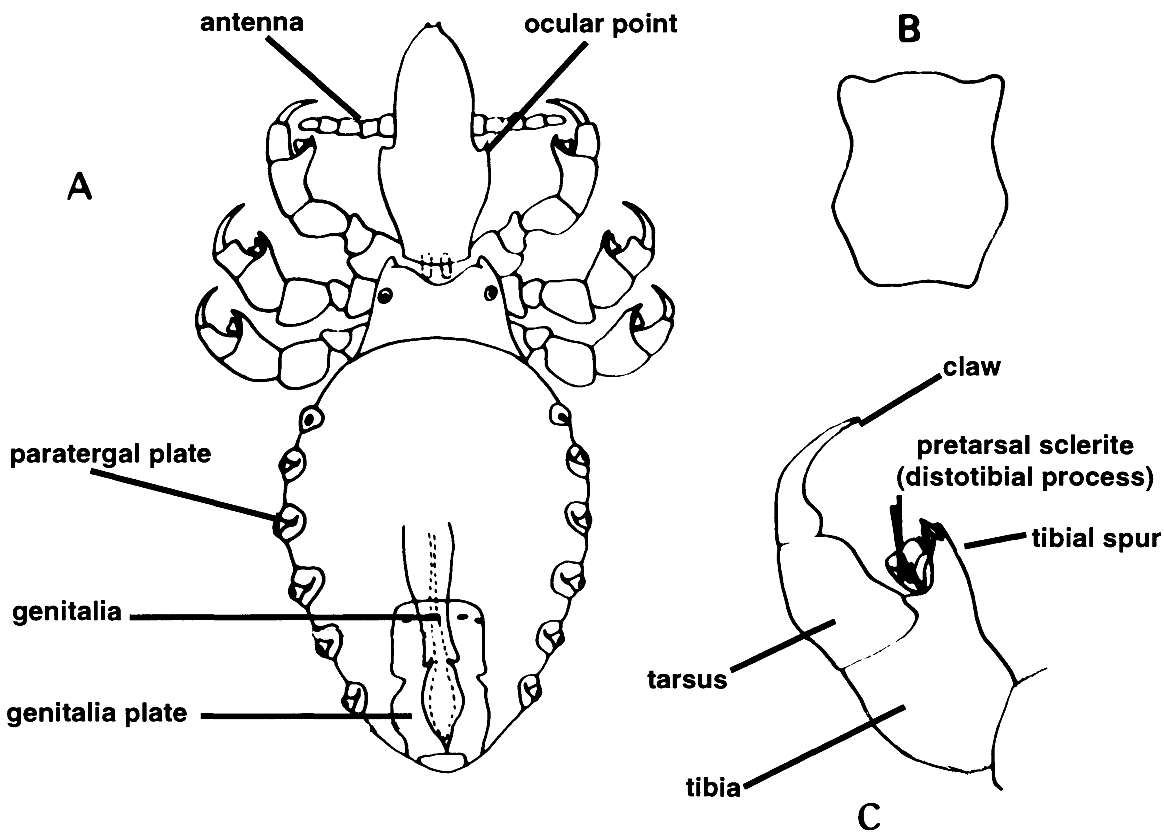


Figure 102. *Haematopinus asini*: ***A***, Adult male; ***B***, outline of sternal plate; ***C***, terminal segments of leg. From Kettle (1984), reprinted by permission of Chapman and Hall, United Kingdom.

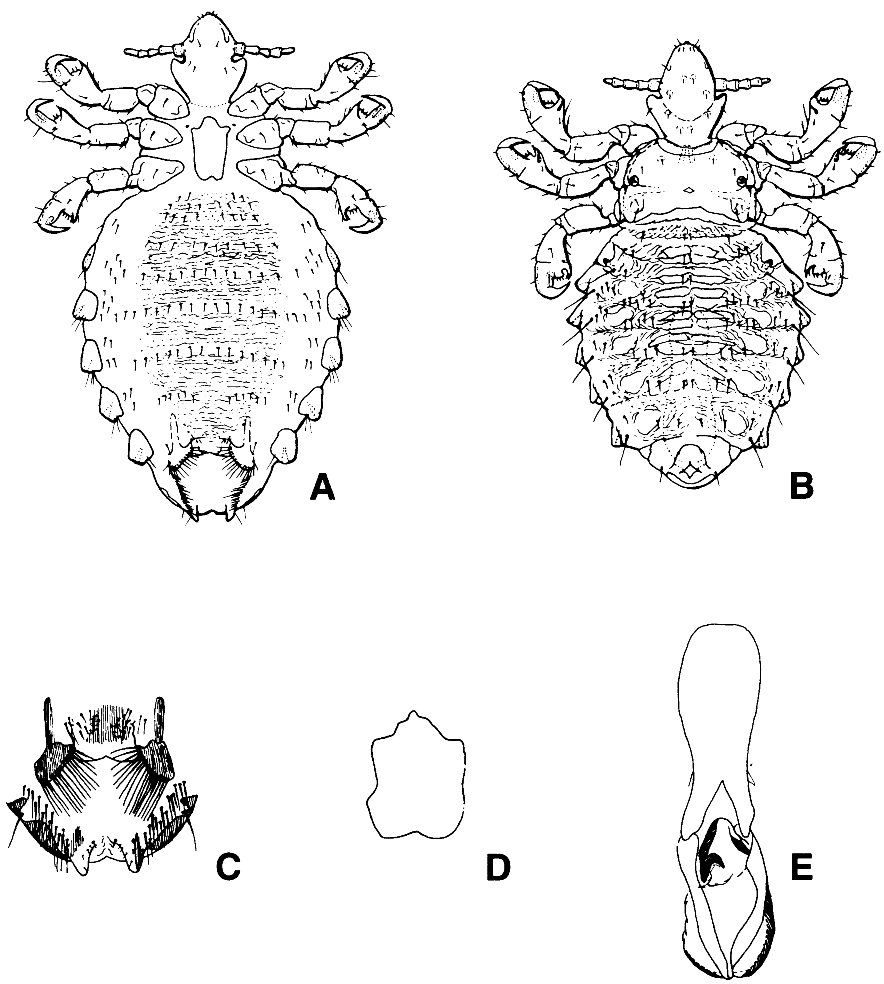


Figure 103. *Haematopinus eurysternus* (shortnosed cattle louse): ***A***, Ventral view of female; ***B***, dorsal view of male; ***C***, female terminalia; ***D***, outline of sternal plate; ***E***, male genitalia. Redrawn with minor modification by Jan Read from Ferris (1951); courtesy of Pacific Coast Entomological Society.

domesticated cattle, and it may be found wherever cattle are raised. This louse has been reliably reported from North America, Europe, Russia, Turkey, Australia, and southern Africa (Meleney and Kim 1974) and from Central America, South America, Asia, the East Indies, and Pacific Islands (Matthysse 1946). In Canada the short-nosed cattle louse is usually the most abundant louse found on range and farm cattle in western Canada, and serious infestations may occur in eastern Canada on feeder cattle that are shipped from the west (Haufe 1962).

Life history. Eggs of *H. eurysternus* are 1.09 mm long (average) and are the longest of the common lice of cattle (*Haematopinus tuberculatus* is excluded). They are usually opaque white, but brownish-white or even brown eggs are sometimes seen. The brown eggs may be newly laid (Craufurd-Benson 1941), so it is not a matter of the eggs changing color after they are laid. The eggs are somewhat pointed at their base. Eggs are attached to a hair near the skin, with the attached end nearest the skin. In winter, when populations of the shortnosed cattle louse are high, the eggs are placed in masses by clusters of females.

In the laboratory, Murray (1957a) constructed a temperature gradient and placed ovipositing females on it. Usually the lice rested in the 32 °C zone in the center of the gradient, but when a female was ready to oviposit, it moved to the warm end and at first faced it. After a few minutes it reversed its position on the gradient, grasped a hair and held it between the gonopophyses and abdomen, rubbed its abdomen up and down on the hair, and then expelled a drop of cement, which was shaped by the gonopophyses as if they were a mold. About 10 sec later, when the cement had started to harden, the louse arched its abdomen, expelled an egg, and then walked away from it. Two or three eggs, laid by different females, may be attached to the same hair.

Although the egg in its natural location is well protected from ambient temperatures, the incubation period is influenced by air temperature. The incubation period in a small cell on a heifer was 14–16 days when the air temperature was 2–3 °C, whereas it was 10–11 days at 9–13.3 °C (Craufurd-Benson 1941). At a constant temperature of 32 °C, eggs removed from a host hatched in an average of 15 days (range of 14–17 days) (Matthysse 1946). In a barn where the temperature fluctuated from −4° to 7 °C, the average incubation period on an animal was 13 days (range of 10–16 days). In the subtropical climate of Queensland (Australia), Roberts (1938a) found that eggs hatched in 11–18 days. Craufurd-Benson found that although relative humidities of 10%–90% did not affect the percentage of eggs that hatched or the length of the incubation period, a relative humidity of either 0% or 100% prevented the eggs from hatching.

Nymphal development of the shortnosed cattle louse was studied by Craufurd-Benson (1941) by placing newly hatched lice in small cells that were cemented onto confined heifers. The animals were held in a stall where the temperature varied from about 3 to 11 °C. In a series of tests, 3–5 days (average 4 days) each was recorded for the first- and second-instar nymphs, and 3–7 days (average 4 days) for the third-instars. Nymphs resemble adults, but nymphs are smaller and paler and they lack genitalia.

When adult *H. eurysternus* eclosed, Craufurd-Benson (1941) found that the male-female ratio was 1:1.3, but apparently males died earlier than females, because the ratio varied from 1:3 to 1:6.6 when adult lice of all ages on an animal were counted. If a male was present, the female mated within a few hours of its emergence, but unmated females laid as many eggs as did mated ones; the only difference was that eggs from unmated females did not hatch. It was suggested that females may mate more than once and that their longevity and oviposition would be extended if they had an opportunity to remate after they had oviposited for a few days.

The preoviposition period was determined by Craufurd-Benson, who found that the female usually begins to lay eggs on the fourth day after emergence. The range was 2–7 days, and the average was 3.6 days. In general, it appeared that the preoviposition period was the same in summer as in winter, but occasionally it seemed to have been shortened by a high air temperature.

The maximum number of eggs laid by a single female in Craufurd-Benson's tests was 24 in a period of 15 days, but he also believed that lice under more natural conditions (not in a cell) produce more eggs. He saw no evidence of parthenogenesis because (1) males were usually present, and (2) females that were in a cell without a male oviposited normally, but their eggs were infertile. A male mated with more than one female if it had the opportunity.

The complete life cycle from egg to egg of a female ranged from 20 to 41 days and averaged 28 days. The longevity of adults in one of Craufurd-Benson's tests was 10 days for males and 16 days for females. It is believed that the shortnosed cattle louse changes hosts when one bovine comes in direct contact with another; but several investigators have attempted to determine (1) how long either the egg or the female louse can live off a host and (2) if a clean animal can become infested from stalls, pens, or trucks that harbor lice. Survival off the host at 20 °C and 70% relative humidity was greater than that at 0–10 °C and 70%–85% relative humidity. More lice (75%–99%) held at the first condition survived 24 hr off a host, while only 27%–33% lived for 48 hr, and 0%–11% for 72 hr.

Allingham (1987) reported an apparent phoretic relationship between *H. eurysternus* and buffalo flies (*Haematobia irritans exigua*) (Diptera: Muscidae) collected in Northern Territory, Australia. Of the flies collected in a light trap, 1 of 8 had a first-instar nymph attached to the femur of a middle leg. Durden (1990a) reviewed phoresy in all Anoplura; the relationship has been reported for two species of *Haematopins*, three species of *Linognathus*, and *Pediculus humanus* (the human louse).

Host-parasite relationships and economic importance. European cattle (*Bos taurus*) are both the type host and the most common host for *Haematopinus eurysternus*. This louse also parasitizes Zebu cattle (*Bos indicus*) (Hopkins 1949). In addition, it has been collected from the eland (*Taurotragus oryx*) under the name *Haematopinus brevipes* (Fiedler and Stampa 1956), a name that Stimie and van der Merwe (1968) synonymized with *H. eurysternus*. As Fiedler and Stampa (1958) pointed out, the eland was in a pasture grazing with domestic cattle, and *H. eurysternus* may have been on it accidentally rather than as part of an established infestation. Mitchell (1979) reported *H. eurysternus* from the nilgai (*Boselaphus tragocamelus*) in the Himalayan kingdom of Nepal.

The shortnosed cattle louse is more abundant on western range cattle than on dairy breeds (Matthysse 1946, Shemanchuk et al. 1960). It appears that the louse prefers Hereford cattle over Angus and also mature over young cattle (Roberts 1952, Scharff 1962, Portus et al. 1977, Butler 1985). *Haematopinus eurysternus* seems to be scarce in tropical zones, but Fairchild (1943) noted "a massive infestation on cattle in Coclé Province, Panama."

During the winter and early spring months, *H. eurysternus* can be found on the top of the neck and withers and perhaps a few on the poll, tailhead, and perineum. If the animal becomes heavily infested, the lice spread to other body regions and may eventually cover the entire body (figs. 104–108). During summer, the lice disappear from the regions of winter preference and are often so scarce that they can hardly be found. But usually a diligent search will reveal a few lice inside the ear near its tip, at the base of the horns, or on the tailhead. Campbell (1992a) suggested that folds of skin between the legs and body of cattle was a summertime site for small numbers of shortnosed cattle lice. Nelson et al. (1975) believed that the movement of aggregations of lice from one body region to another indicates the development of localized acquired resistance. Craufurd-Benson (1941) distinguished between what he called "breeding colonies" (females and their eggs) and "nymphal clusters," and indicated that lice of the two ages may prefer different attachment sites.

Large numbers of lice cause cattle to have a greasy appearance, presumably because of louse excreta on the hair coat. Infested animals are constantly irritated by the presence of the lice, by their feeding activity, and by the itching they cause; as a result, the cattle spend considerable time rubbing and scratching themselves instead of grazing. These activities lead to loss of hair, the skin becomes scaly, and raw areas eventually appear. The large sores and scabby areas reduce the animal's vitality and render it more susceptible to inclement weather and disease. In extreme cases, especially in combination with malnourishment and disease, the animal may die.

Freer and Gahan (1968) differed from most investigators because they found that, under their conditions, even low levels of infestation with the shortnosed cattle louse interfere with weight gains. In a trial carried out in New South Wales for 100 days, they found that the spraying of lightly infested steers resulted in an increased gain of 40 lb/steer over the gain made by comparable unsprayed steers.

Peterson et al. (1953) found that cattle severely infested with *H. eurysternus* are often anemic and if not treated, will die. The hematocrit values (red blood cell volume) of blood samples from range cattle in New Mexico dropped to as low as 9% and averaged 11.4% while cattle were heavily infested with lice, but the values rose to more than 35% in 39–44 days after the cattle were sprayed with an insecticide to control the lice. Very similar results were reported by Shemanchuk et al. (1960), who studied groups of 23 louse-infested and 19 comparable louse-free mature cattle in Alberta. Their results indicated an approximate 50% reduction in the number of erythrocytes and in the quantity of hemoglobin in louse-infested cattle. Collins and Dewhirst (1965) in Arizona confirmed earlier findings with heavily infested range cattle whose packed cell volume was only 59.4% of that of comparable animals which were either louse-free or only lightly infested. Scharff (1962) also concluded that highly susceptible cattle are at risk of death caused by anemia, but he decided that in Montana, only 1%–2% of cattle have such high susceptibility. DeVaney et al. (1992) noted that a group of calves infested with *Haematopinus eurysternus* (and *Bovicola bovis* and *Linognathus vituli*) weighed 11.4 kg less than uninfested controls at the end of two trials in Texas. Bolte (1992) stated that recent studies showed that heavy louse infestations (10 or more per inch^2) decrease weight gains significantly, whereas light or moderate infestations do not.

Ely and Harvey (1969) demonstrated that the number of lice on cattle is influenced by their ration. They divided 90 steers into groups of 10, and each group was provided a different ration. At one extreme of nutrition was the control group, which received sorghum silage alone;

Figure 104. Infestation sites and incidence of *Haematopinus eurysternus*. Eggs, nymphs, and excreta can be seen on dewlap. Adults are plentiful around bare spot on side of neck. Courtesy of Texas A&M University.

Figure 105. Infestation sites and incidence of shortnosed cattle lice. Lice are feeding around bare spot caused by cow rubbing against posts and trees. Courtesy of Texas A&M University.

Figure 106. Infestation sites and incidence of shortnosed cattle lice. Adults and nymphs cling to hairs in and around bare spot. Courtesy of Texas A&M University.

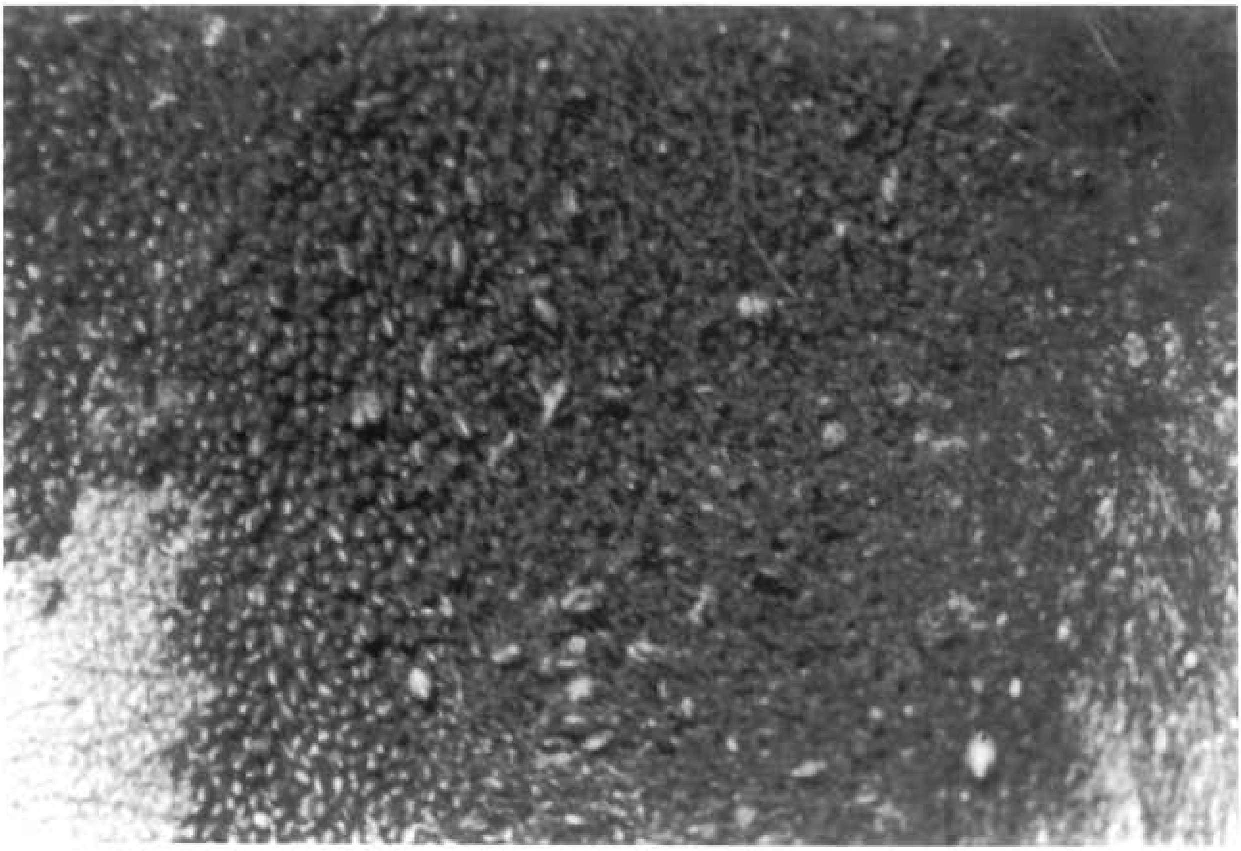


Figure 107. Closeup of same lice seen in fig. 106. Courtesy of Texas A&M University.

Figure 108. Infestation sites and incidence of *Haematopinus eurysternus.* Large numbers of lice have attached to hair on tail. Courtesy of Texas A&M University.

this resulted in an average 190.3 lice per animal. At the other extreme was a group that received sorghum silage plus cottonseed meal and sorghum grain; this resulted in an average 11.4 lice per animal. These two extremes also provided the least average daily gain (0.10 lb) and the greatest average daily gain (0.74 lb).

It is not known why certain animals, perhaps 1% or less of a herd, are so highly susceptible that they have shortnosed cattle lice on them year-round. These animals, known as louse "carriers," must either be treated by the owner or culled from the herd. These cattle not only have a tremendous louse load in winter but continue to have large numbers in summer, when it is difficult to find lice on most cattle. Nelson et al. (1970) observed that carrier cattle usually had eosinophil counts above 400/mm^3, whereas both louse-resistant and extremely louse-susceptible cattle usually had counts of less than 200/mm^3. It was suggested that a severe allergic reaction operated to maintain a high eosinophilia in carrier cattle even during periods of low louse counts.

Cattle may be infested with *H. eurysternus* alone or in combination with one or more other species of lice, and where mixed infestations occur, it is quite difficult to identify the damage done by a particular species. But it is generally agreed that in areas where it is abundant, *Haematopinus eurysternus* is the most damaging species.

Haematopinus quadripertusus (cattle tail louse)

In addition to its other characteristics, the larger size of *Haematopinus quadripertusus* can be used to distinguish it from *H. eurysternus.* A group of female cattle tail lice were measured by Meleney and Kim (1974) and found to be 4.54 mm long (range of 4.27 to 4.75 mm), whereas a comparable group of shortnosed cattle lice were 3.09 mm long (range of 2.94 to 3.18 mm). Kim et al. (1986) stated that the mean lengths of the female cattle tail louse and the female shortnosed cattle louse are 3.99 and 2.88 mm, respectively. Although larger than *H. eurysternus, H. quadripertusus* is usually smaller than *H. tuberculatus.* The head of *H. quadripertusus* is more elongated than the heads of the other two *Haematopinus* of cattle. The anterolateral (front corners) and median projections of the thoracic sternal plate of *H. quadripertusus* are quite pronounced, especially in males (figs. 109, 110). The tracheal trunks are thickened. The median subgenital plate is shorter and broader, and the ninth abdominal tergite has a blunt anteromedial projection (figs. 111, 112). The male subgenital plate has only three or four small setae. The head, thorax, and legs are dark brown—darker than in *H. eurysternus*—and the abdomen is dark gray (Roberts 1952).

The cattle tail louse is a tropical species that has been reported from Cameroun by Fahrenholz (1916); from the Congo by Benoit (1964); Queensland, New Guinea, and the Solomon Islands by Roberts (1950); Puerto Rico by Maldonado-Capriles and Medina-Gaud (1971); Texas, Alabama, and Florida by Becklund (1964); Mexico, Costa Rica, Panama, Venezuela, Africa (south of the Sahara), Madagascar, Ceylon, Malaysia, Taiwan, and the Seychelles Islands by Meleney and Kim (1974); and tropical India (Bangalore) by Rao et al. (1977). From their examination of 1,053 cattle in Libya, Gabaj et al. (1993) found that 330 were infested with sucking lice and that *H. quadripertusus* was the predominant species. No *H. eurysternus* were collected in that survey.

Haematopinus quadripertusus is a tropical species that has extended its distribution into subtropical areas such as the Gulf Coast of the United States and into Queensland, Australia. It is apparently unable to establish itself in either temperate or cold climates. It was said to differ from other cattle lice in that higher numbers are present in the summer, not the winter (Melancon 1993). Butler (1985) mentioned that the cattle tail louse is believed to have been introduced into Florida from Africa in 1945.

Life history. The eggs of the cattle tail louse are deposited almost exclusively on the hairs of the tail switch, where the females lay one or two eggs per day, and only a few scattered eggs can be seen on the tailhead and on the ears. The eggs are 0.76 mm long by 0.32 mm wide (Butler 1985). Apparently, after they hatch, the immature lice leave the switch and move to other parts of the body to feed, especially on the tender parts of the body such as the perineum and vulva. It is possible that the third-instar nymphs move back to the tail just before they molt; Bruce (1947) and Creighton and Dennis (1947) mentioned seeing a few third instars on the tail. The incubation period is at least 9 days and may be as many as 25 days during cooler weather (Meleney and Kim 1974). Roberts (1952) said that the average incubation period is 11 days in Queensland, Australia.

The life cycle egg to egg may be as short as 25 days but is usually longer because the incubation period is prolonged. When the cattle tail louse was fed on humans experimentally, lice fed every 4 hr (Butler 1985). Apparently a complete life history has not been reported for this species.

Host-parasite relationships and economic importance. When Fahrenholz (1916) described *Haematopinus quadripertusus* in German, he merely stated that the host was "Rinder," or cattle. The louse is known to parasitize both European and zebu cattle, and Meleney

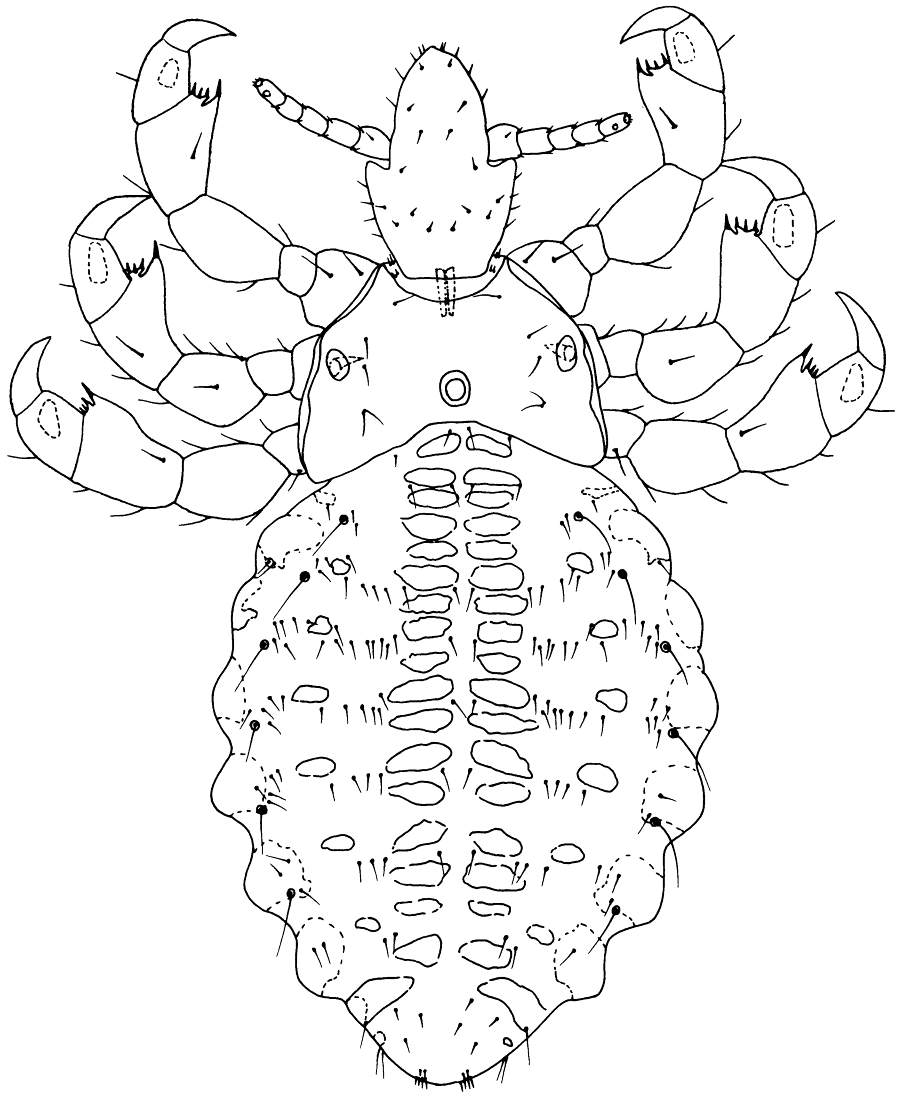


Figure 109. *Haematopinus quadripertusus* (cattle tail louse): Dorsal view of male. Original drawing by Wen Sam Wang; courtesy of Texas A&M University.

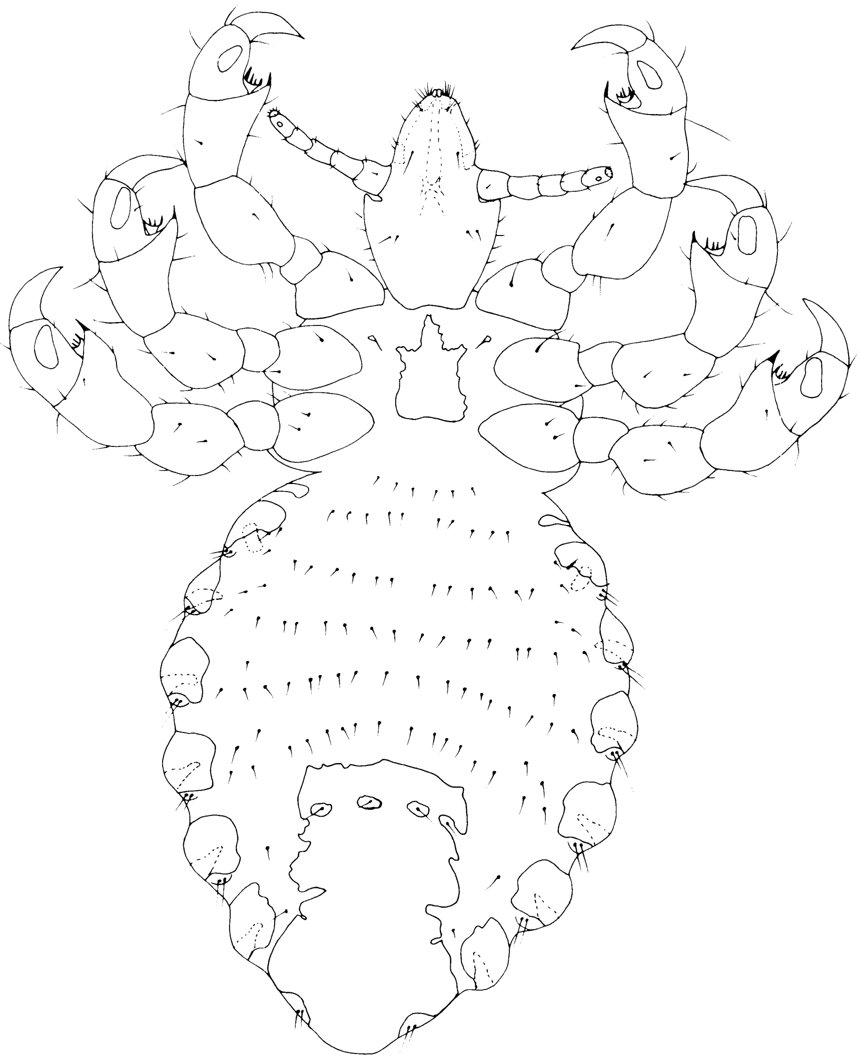


Figure 110. *Haematopinus quadripertusus*: Ventral view of male. Original drawing by Wen Sam Wang; courtesy of Texas A&M University.

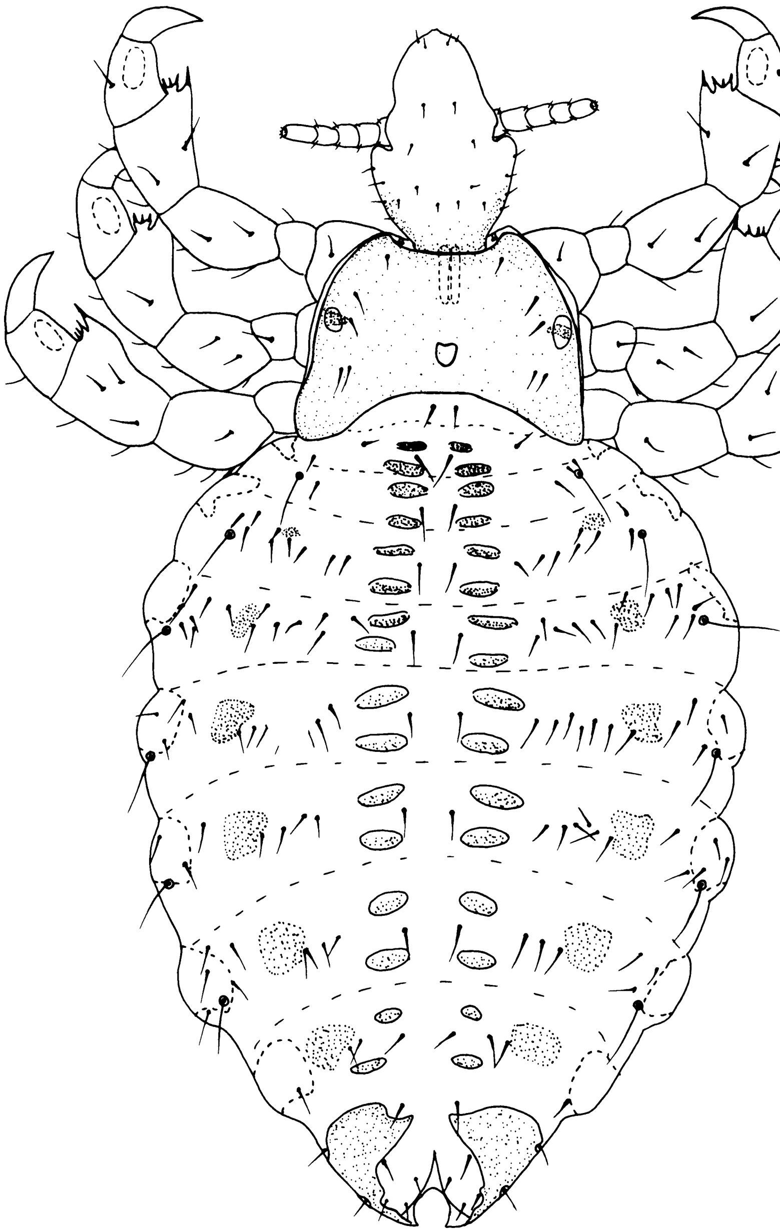


Figure 111. *Haematopinus quadripertusus*: Dorsal view of female. Original drawing by Wen Sam Wang; courtesy of Texas A&M University.

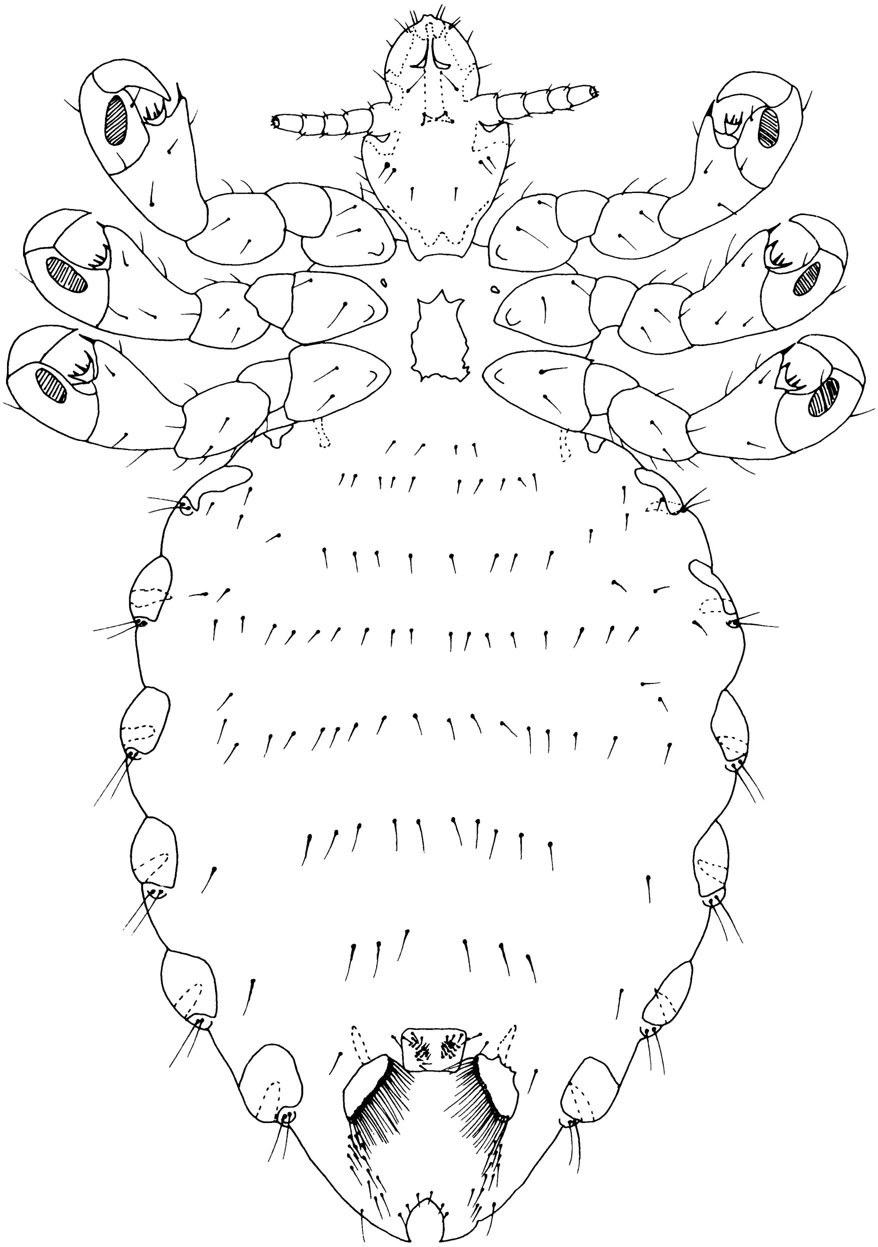


Figure 112. *Haematopinus quadripertusus*: Ventral view of female. Original drawing by Wen Sam Wang; courtesy of Texas A&M University.

and Kim (1974) regarded zebu cattle as the type host. However, the louse now seems to thrive well on either host. Bruce (1947) and Creighton and Dennis (1947) described it as a serious pest, which livestock owners feared more than other cattle lice. Severe infestations were said to have a devitalizing effect on cattle, which left them emaciated. Butler (1985) stated that a heavily infested animal may shed its tail.

Since 1947 it seems that this louse has not extended its distribution in the United States. Perhaps because of the availability of modern insecticides, it is now less threatening. More recent opinions are much more conservative than those of Bruce or Creighton and Dennis; Maldonado-Capriles and Medina-Gaud (1971) found the cattle tail louse on 59 of 60 dairy farms in Puerto Rico, but saw only two infestations serious enough to cause sloughing of the epidermis and loss of tail hair.

***Haematopinus suis* (hog louse)**

The only louse, either chewing or sucking, that parasitizes domestic swine is *Haematopinus suis* (fig. 113). It is one of the largest *Haematopinus* found on domestic animals, sometimes measuring 5–6 mm long. The head is at least twice as long as wide. The sternal plate is wider than long (fig. 114) and has sternal pits and anterolateral and posterolateral projections, but the projections are not prominent. The abdomen has crescent-shaped paratergal plates that occupy at least three-fourths of each segment and form a dark band along the sides of the abdomen (fig. 115).

The hog louse has the same cosmopolitan distribution as its host, the domestic hog, but is most prevalent in temperate climates (Butler 1985).

Life history. Like all Anoplura, *H. suis* is an obligatory parasite that spends its entire life on its host. The eggs are white when first laid but gradually turn to light amber (Florence 1921). The egg is cemented to a hair on the host with the narrow end down, nearest the host, and the operculum pointed upward (fig. 116). When a pig is heavily infested, females will lay more than 1 egg on a single hair; Watts (1918) counted as many as 26 eggs. When present in large numbers, the eggs are quite conspicuous (fig. 117). Throughout the midwestern United States, the lice are most abundant in winter, and the maximum numbers of eggs are likely to be seen in December to March (DeWitt 1975).

Using the scanning electron microscope, Hinton (1977) studied the structure of the hog louse egg and found that the chorion of the eggshell is present as two sheets and that the space between them is a web of air chambers that functions as a reflector (fig. 118). This provides protection from direct sunlight for the eggs, as the hog often lies in the sun for prolonged periods of time.

The incubation period is usually 12–14 days but may be extended to 20 or more days in cold weather (Watts 1918, Florence 1921, Cobbett and Bushland 1956). When ready to eclose, the first-instar nymph pushes open the operculum. It uses body movement to exert pressure on the operculum and also uses the hatching organ [referred to as the egg burster in other orders of insects (Kumar and Sommadder 1976)] to cut the middle membrane of the eggshell.

The newly emerged nymph moves to a tender part of the host's body, such as inside the ear, and begins to feed. First-instar nymphs of the hog louse are very light colored and almost transparent; the body is pale yellow and the mouthparts and claws are brown (Watts 1918). They molt after 5–6 days, second instars after 4 days, and third instars after 4–5 days at a constant 35 -C (Florence 1921). The 13–15 days reported by Florence for development of the immatures is quite compatible with the 10–12 days reported by Watts, 14 days by DeWitt (1975), and 10–12 days by Kemper and Peterson (1955) and Cobbett and Bushland (1956).

The feeding behavior of nymphs is the same as that of adults, which has been described by Lavoipierre (1967). After lice had been starved overnight, they fed readily on a mouse's ear under the microscope (fig. 119). The haustellum was everted and pushed into the epidermis of the ear using the buccal teeth as a cutting organ. Once the haustellum was in place, the buccal teeth were used to anchor it. The stylets were pushed out and used to probe the tissue until a blood vessel was encountered. The tips of the stylets were pushed into the lumen of a venule, but the louse may have probed several times before a venule was found. The stylets usually turned out at an angle, perhaps to as much as 45°. Florence (1921) and Stojanovich (1945) described the stylets in detail.

Usually about 10–15 min were needed for the insect to obtain a full blood meal. The hog louse is a true solenophage (vessel feeder); it does not feed from a pool of blood in the epidermis as do many other hematophagous insects. A hematoma is never seen where the louse has fed in the epidermis.

Florence (1921) described the act of molting in detail: When ready to molt, the immature louse raises itself until only the posterior end of the abdomen and the claws of the second pair of legs are touching the object on which the louse is resting. The back has a humped appearance, and the head is bent down at a right angle to the body. The old integument then ruptures along a median longitudinal line on the dorsum, helped by the

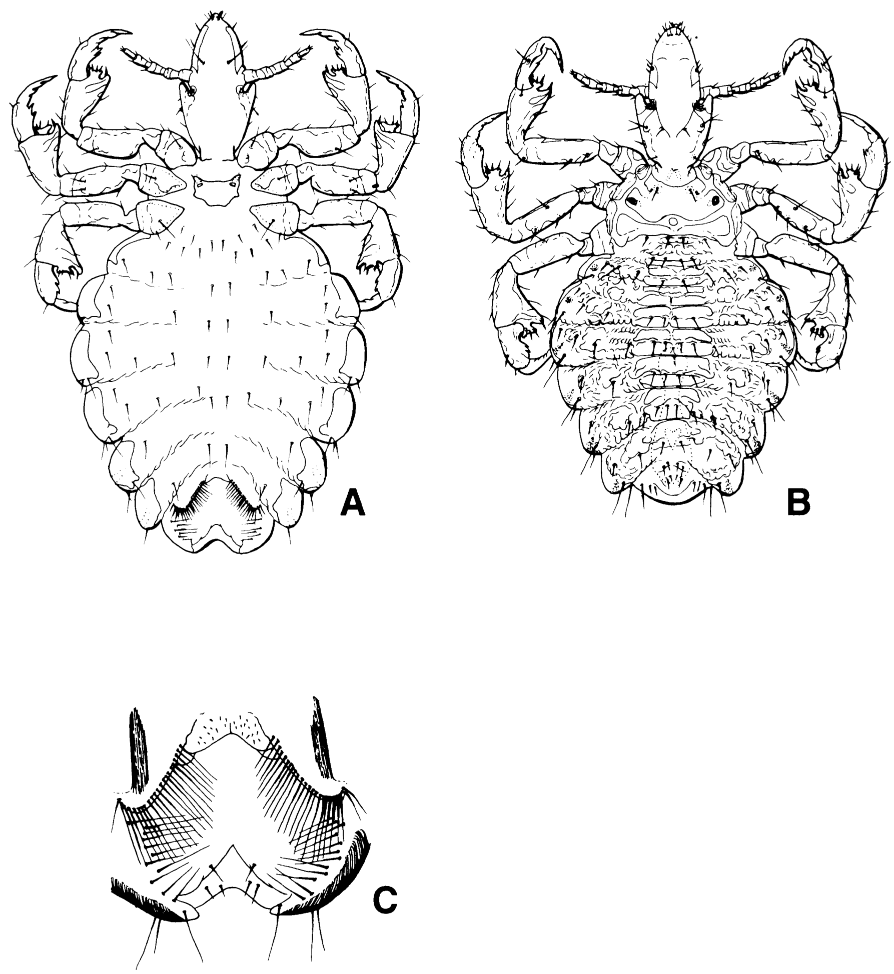


Figure 113. *Haematopinus suis* (hog louse): ***A***, Ventral view of female; ***B***, dorsal view of male; ***C***, female terminalia. Redrawn with minor modification by Jan Read from Ferris (1951); courtesy of Pacific Coast Entomological Society.

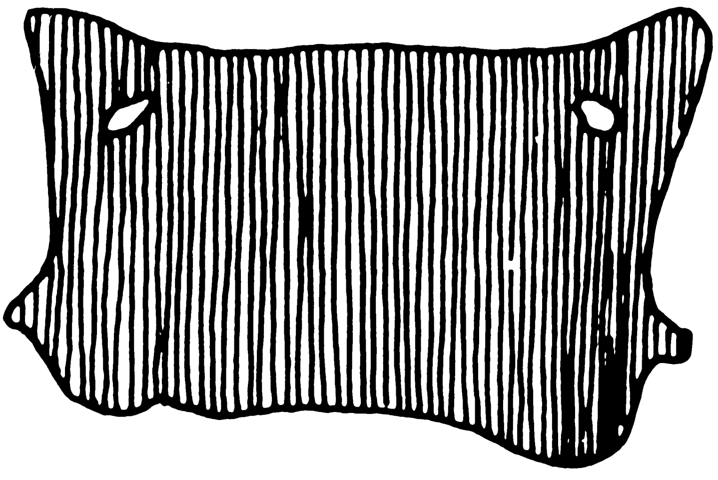


Figure 114. *Haematopinus suis*: Thoracic sternal plate. From Kim and Ludwig (1978a), reprinted by permission of Blackwell Science Ltd, Oxford, United Kingdom.

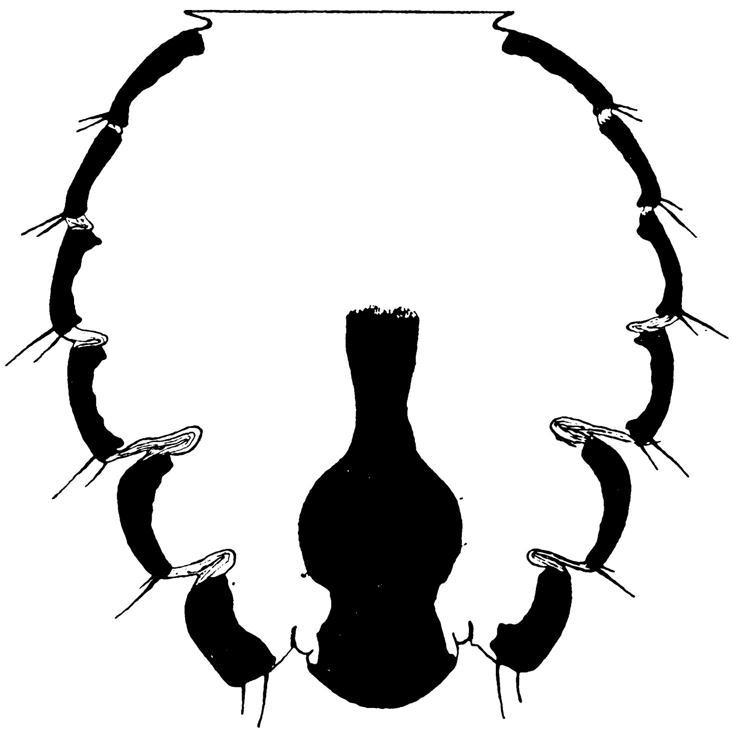


Figure 115. Male hog louse. Black streak on underside of abdomen of male hog louse is not found on female. From Watts (1918), reprinted by permission of University of Tennessee Agricultural Experiment Station.

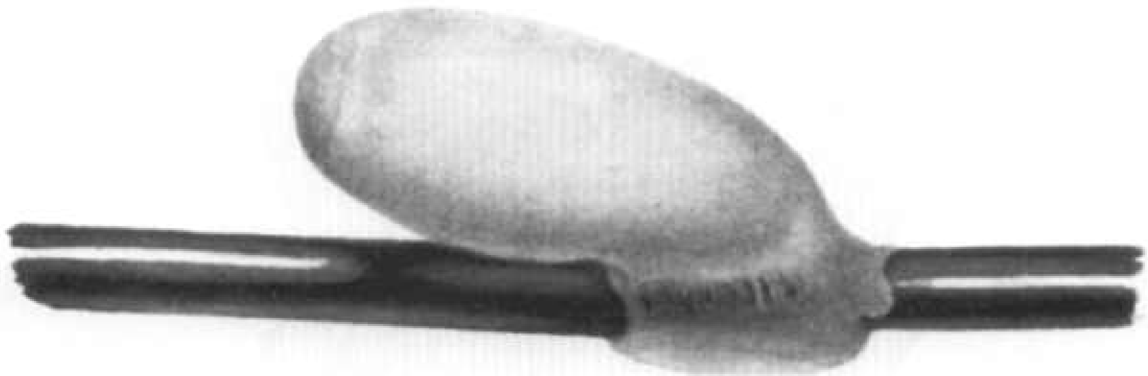


Figure 116. Egg of *Haematopinus suis* attached to a hog hair. Reproduced from Agriculture and Agri-Food Canada [fig. 62 (egg of hog louse) in Hearle (1938)] by permission of Minister, Government Services Canada. Drawn by Frank Hennessy.

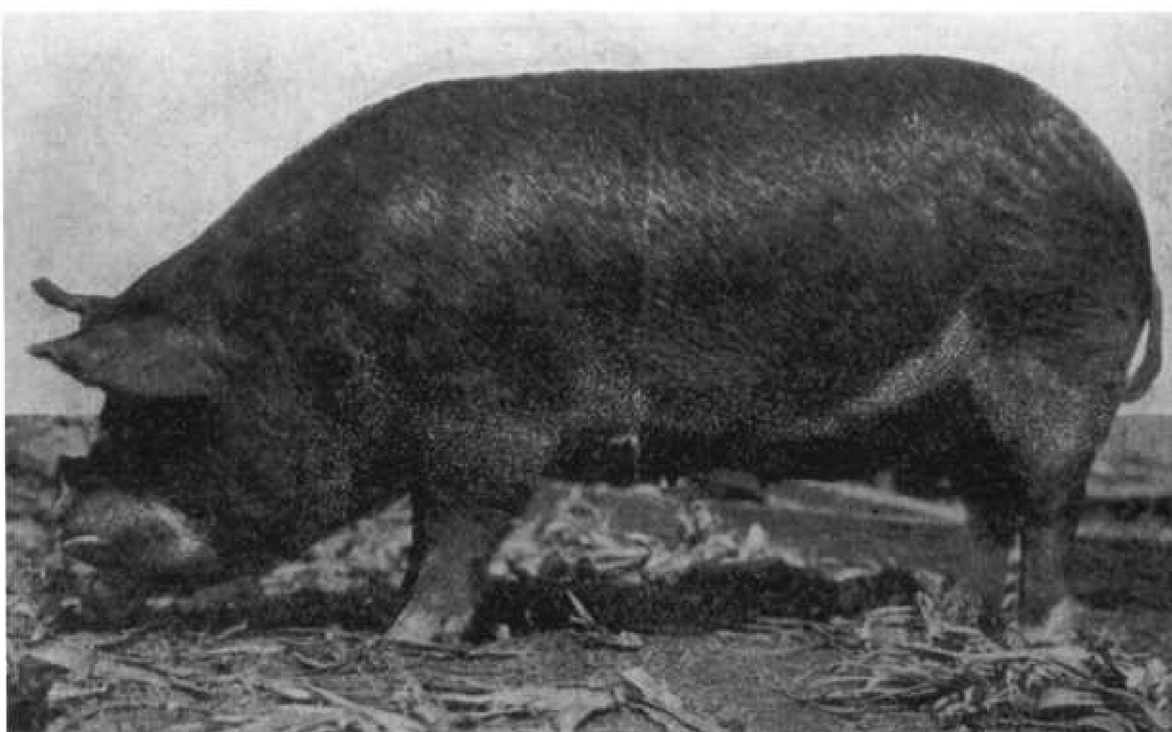


Figure 117. Band of eggs of *Haematopinus suis* across lower neck, upper legs, and abdomen of a hog. From Watts (1918), reprinted by permission of University of Tennessee Agricultural Experiment Station.

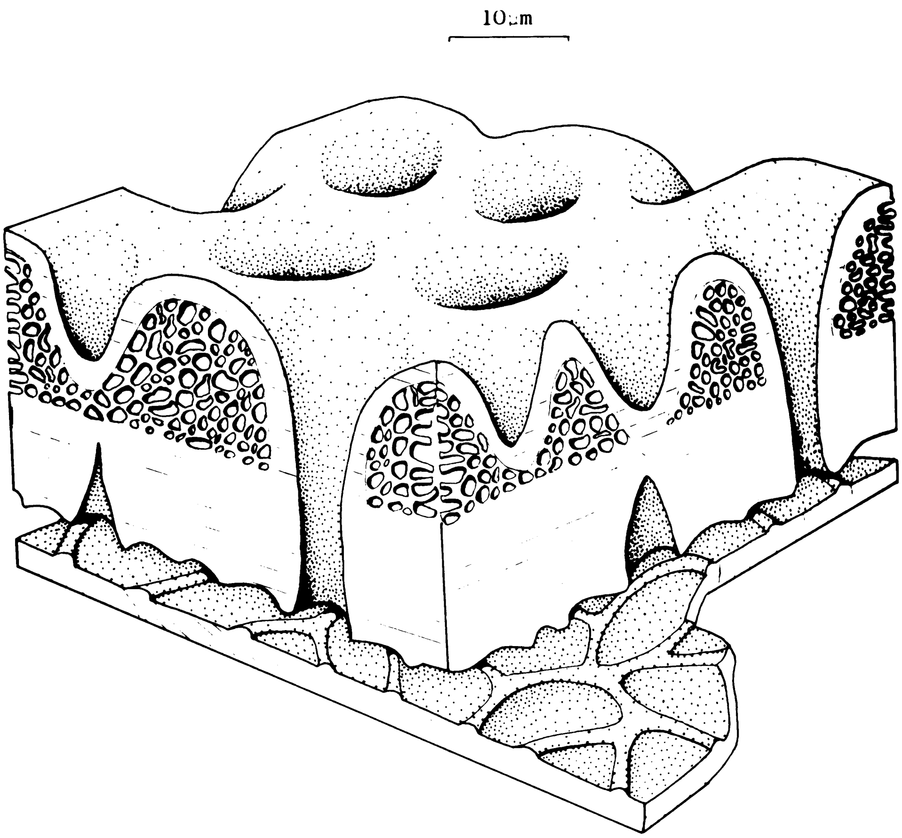


Figure 118. Cross section through shell of egg of hog louse (note scale). Drawn from SEM's in Hinton (1977), Journal of Insect Physiology, © 1977, with permission from Elsevier Science Ltd, Kidlington, United Kingdom.

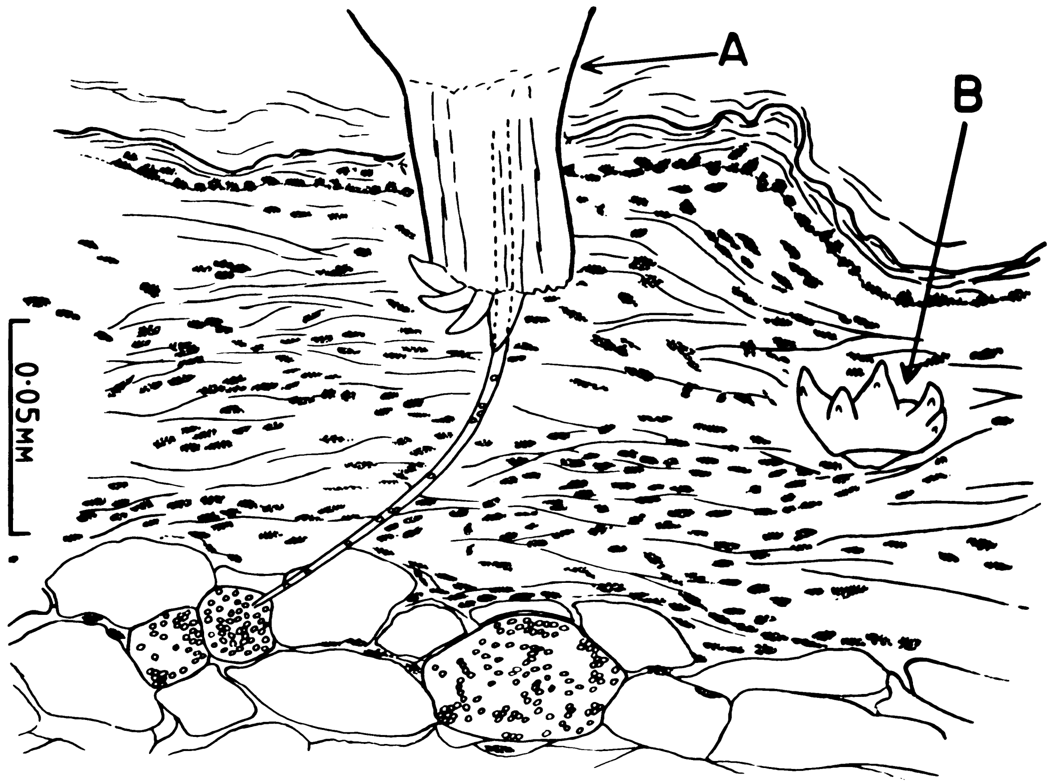


Figure 119. Mechanism of feeding in *Haematopinus suis*. ***A***, Proboscis is anchored in dermis by everted buccal teeth, and stylets are inserted into a venule; ***B***, lateral view of everted buccal teeth. From Lavoipierre (1967), reprinted by permission of Academic Press Ltd, London.

air that the louse swallows and expels through the anus. The head and thorax are gradually pushed out through the split in the old integument, which by this time has taken on the appearance of a T. The first pair of legs are then withdrawn and these, by pushing down on the old integument, help to free the head and mouthparts. After the head assumes its normal position, the second and third pair of legs are withdrawn, and the newly emerged louse is free to walk away from its old integument, which remains attached to a hair. For the molt that Florence observed, a period of 30 min elapsed from start to finish.

Whether mated or not, a *Haematopinus suis* female begins to lay eggs after a preoviposition period of 3 days at the rate of three to six per day for the remainder of the female's life. It has been estimated that a female lives for 25 days and produces a total of 90–150 eggs in her lifetime. Williams (1985) suggested that adults may live as long as 5 wk and lay three to six eggs per day. Florence (1921) observed that unmated females deposit eggs but that those eggs never hatch. Because males and females are usually present in approximately equal numbers, parthenogenetic reproduction is very unlikely.

Tombesi and Papeschi (1993) reported a cytogenetic study revealing that *H. suis* has a chromosome number of 2n=10; the low number was believed to be one of the reasons that genetic variability is minimal.

The hog louse has a peculiar method of locomotion: It usually moves about through the bristles on the host by moving sideways. Lice readily transfer from one hog to another, and suckling pigs quickly acquire lice from their dams. Off the host, lice do not live very long; it is believed that nearly all that are lost from swine die within 2–3 days.

Watts (1918) estimated the average longevity of a female hog louse to be 30 days (range of 15 to 40 days). Florence (1921) reported a maximum lifespan of 35 days for lice carried in glass vials close to a human body and a life cycle from egg to egg of 29–33 days. Typically there are 6–12 generations per year (Williams 1986).

Host-parasite relationships and economic importance. The taxonomic status of both *Haematopinus suis* and its hosts in the family Suidae remains confused. The louse was described by Linnaeus in 1758, and many modern taxonomists assume that his specimens came from domestic swine in Sweden. Others feel sure that the louse he described had been collected from the European wild boar, a species that may differ from that of domesticated swine in Europe. [It is possible that domestic swine in Europe were developed from an Asiatic species of Suidae, *Sus cristatus*. However, Mochi and Carter (1971) considered *S. cristatus*, the Indian wild boar, to be a subspecies of *Sus scrofa*.] Stimie and van der Merwe (1968) accepted Ferris' (1951) contention that *Haematopinus apri (=aperis)* is the sucking louse of the European wild boar (*S. scrofa*). Kadulski (1974) reported the collection of *H. apri* from 184 of 527 wild boars at 60 localities in 17 provinces of Poland. Louse incidence was much higher in young boars than in adults; in October the average number of lice per infested young animal was approximately 50. However, K.C. Emerson identified lice collected by Henry and Conley (1970) from European wild hogs in Tennessee as *H. suis*. In addition, Ansari (1951) reported *H. suis* from the Indian wild boar, which he identified as *S. cristatus*.

Since the question remains unsettled, both *H. suis* and *H. apri (=aperis)* are listed in our appendix B. It appears that the question can be resolved only by crossing *H. apri* with *H. suis* in the laboratory and observing the fertility of their progeny.

Wooten-Saadi et al. (1987) examined 1,994 pigs in a market survey and found that 18.1% were infested with *H. suis*. Of the 361 infested pigs, most had 24 or fewer lice, but 12 pigs had 100–499 lice and 8 pigs had more than 500 lice.

The sucking of blood by the hog louse irritates the host's skin and causes it to itch. The lice feed frequently, and they puncture the skin and suck blood in a different place each time. When the mouthparts are first inserted, the animal feels a sharp, stinging sensation, which causes the hog to rub. Lousy hogs often rub to such an extent that the skin is scratched or torn in small places and blood seeps out. Then these injuries in turn attract lice; 50 or more lice may be seen closely packed around a single wound. The growth of young pigs may be arrested by heavy infestations.

Frequent rubbing and scratching causes the skin to become rough and scaly and hogs to lose vitality (Cobbett and Bushland 1956). Lousy hogs become restless and eat less, which interferes with their growth. In addition, anemia caused by blood loss may occur, especially in young pigs. Hog lice attack swine of any age or condition, including both domestic and wild hogs almost worldwide.

Both eggs and lice can be found on all parts of a heavily infested hog. Immature lice are frequently found on the inside of the animal's ears, often deep inside the inner canal. Other protected places are on the tender skin behind the ears (Bay and Harris 1988), in the folds of the neck, on the inside of the legs close to the body, and in the inner flanks. Lice of all ages are commonly found under the scurf (scales) of the skin, where in winter they are protected from the cold air and kept warm by the skin beneath them. They are found in the same location in summer, but especially on upper parts of the body. In this way, the lice apparently contact the newer skin and feed on it.

It is claimed that *H. suis* can transmit swine pox virus *(Eperythrozoan suis)* and other diseases to susceptible pigs (McKean and DeWitt 1978, Durden and Musser 1994b). This louse has also been incriminated as a potential vector of other diseases such as hog cholera and eperythrozoonosis (Williams 1985). After pigs were treated to eliminate lice from a swine herd in Missouri, both cutaneous streptococcal abscesses and swinepox were also eliminated (Miller and Olson 1978).

The value of an infested animal declines by 2%–6% (Babcock and Cushing 1942b). Williams and Gaafar (1988) noted that annual losses caused by the hog louse in the United States were $40 million.

Haematopinus tuberculatus

In several textbooks, the authors have referred to *Haematopinus tuberculatus* as the buffalo louse because its natural host is the water buffalo (*Bubalus bubalis*). This large louse apparently varies in size; Roberts (1952) stated that Australian specimens were 5.5 mm long, whereas Ansari (1951) in India measured females that were 2.5–3.6 mm long and males 2.9 mm. (Differences in measuring techniques were probably the cause of this discrepancy.) The sternal plate is almost rectangular, and its anterolateral arms are distinct (figs. 120, 121). The paratergites are enlarged and more elongated than those of *Haematopinus eurysternus* or *H. quadripertusus*. Just behind each paratergite are large setae—usually seven or eight but at least five or six. The gonapophyses are elongate and curved, and they taper posteriorly (Stimie and van der Merwe 1968). Quadri (1948) described the external and internal anatomy of *H. tuberculatus* in detail.

Haematopinus tuberculatus has accompanied water buffalo, its type host, to many tropical countries. The louse has been reported from Queensland and Northern Territory in Australia, Philippines, China, Thailand, Pakistan, India, Iraq, Russia, Madagascar, French Guiana, and Guam, and probably occurs wherever its host is present in large numbers. Reports of *H. tuberculatus* from Brazil (Laake 1949) and Puerto Rico (Van Volkenberg 1934) may have been reports of misidentified *H. quadripertusus*.

Life history. An egg of *H. tuberculatus* is deposited on a single hair of its host, but as many as six or seven eggs may be seen on one hair. Eggs are usually deposited on the shoulders, neck, and forelegs of the host even though the lice are more likely to be found on the back and hindlegs. The egg is oval and somewhat pointed at its base; it is white when first deposited but slowly turns to brownish white. It is about 1.2 mm long and 0.6 mm wide (Chaudhuri and Kumar 1961).

During winter in India, the incubation period may be 11–12 days but is more likely to be 9–11 days. Chaudhuri and Kumar noted that relative humidity has little or no influence on the incubation period of eggs on a water buffalo.

Haematopinus tuberculatus has three nymphal instars, each of which requires 3 or 4 days (usually 4 days) for development. The preoviposition period is 2–3 days. A female may lay 1–8 eggs per day for 10–20 days and a total of 62–93 eggs in its lifetime.

Chaudhuri and Kumar (1961) found that under their conditions, the life cycle from egg to egg requires an average of 24 days (range of 21–27 days). Mehrotra and Singh (1981) calculated that the life cycle required 23 days, with hatch occurring after 11 days and 3 days required by each nymphal instar to complete its development.

As is true for many other lice, the population of *H. tuberculatus* builds up in winter (December and January in the Northern Hemisphere) and reaches a peak in February. In March the population begins to decline, and very few or no lice can be found in June and July.

Host-parasite relationships. The Asiatic water buffalo or carabao (*Bubalus bubalis)* is both normal and type host for *H. tuberculatus*. Roberts (1935, 1938a, 1950) stated that it had also become fully established on cattle in northern Queensland, Australia. Stimie and van der Merwe (1968) reported it from cattle in Burma that had not had any recent contact with water buffalo. It appears to have transferred to cattle in various parts of the world and to be able to maintain itself on cattle in tropical climates, but it does not appear that cattle are a normal host. The yak (*Bos grunniens*) was added to the host list by Ferris (1951). Roberts (1952) stated that *H. tuberculatus* had also been collected from camels in northwestern Australia, and Stimie and van der Merwe provided several records from camels in Egypt. Nevertheless, records of *H. tuberculatus* from Camelidae (Perissodactyla) seem to be an exception to the general rule about host relationships. Reports of the buffalo louse from a dog in Thailand and from a sheep in the Philippine Islands were probably based on the collection of stragglers.

It should be noted that Chaudhuri and Kumar (1961) were unable to infest calves and goats by transferring large numbers of *H. tuberculatus* onto them. Yeruham et al. (1993) reported that individual lice were observed crawling about on the skin of buffaloes and cattle and

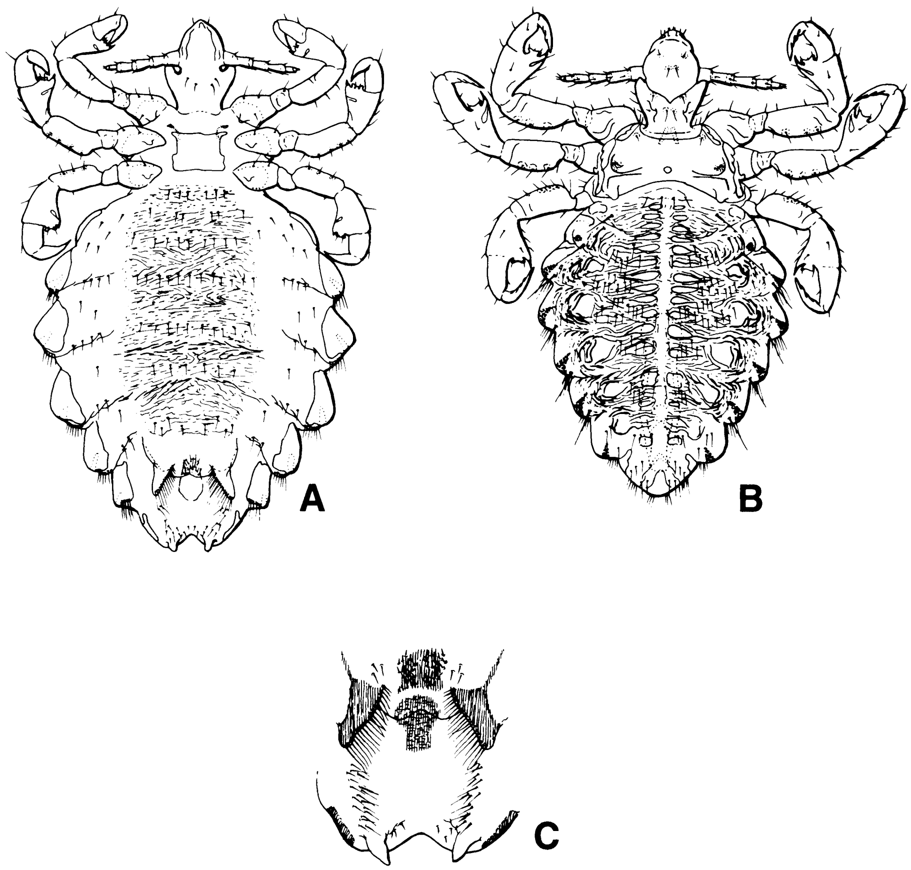


Figure 120. *Haematopinus tuberculatus*: ***A***, Ventral view of female; ***B***, dorsal view of male; ***C***, female terminalia. Redrawn with minor modification by Jan Read from Ferris (1951); courtesy of Pacific Coast Entomological Society.

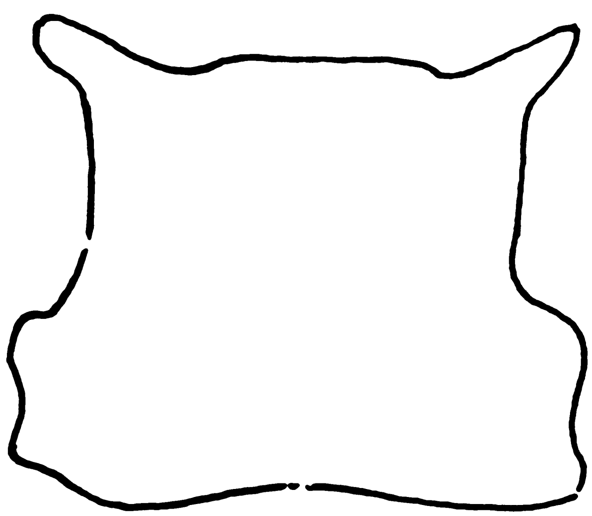


Figure 121. Thoracic sternal plate of *Haematopinus tuberculatus* is almost rectangular, and its anterolateral arms are distinct. From Ferris (1951), reprinted by permission of Pacific Coast Entomological Society.

did not seem to have a favored attachment site. Even during the months that populations are highest, it appears that infested water buffalo and cattle never have tremendous numbers of lice on them; as a result, the buffalo louse seldom causes serious damage. Usually only a few lice can be found on the head, ears, or tail of water buffalo. However, Chaudhuri and Kumar described the skin irritation produced by the lice in buffalo calves; they stated that lousy calves may rub and bite themselves enough to produce bald areas and raw spots, which are then exposed to blowflies and invasion by bacteria. Also, Lau et al. (1980) stated that lice cause restlessness, loss of appetite, malnutrition, and anemia when present in large numbers on water buffalo in Para, Brazil.

Other species of *Haematopinus*

Kim et al. (1990) estimated that the genus *Haematopinus* contains 20 species; we list 19 here in appendix B. In addition to the 5 species discussed in this text, 14 other species of *Haematopinus* parasitize large game animals in the families Bovidae, Cervidae, and Suidae. Most of these animals occur in the Ethiopian Zoogeographical Region.

Horak et al. (1992a) collected small numbers of *Haematopinus oryx* from gemsbok (*Oryx gazella*) in national parks in Namibia.

Apparently the life history and host-parasite relationships of the other 14 species of *Haematopinus* have not been studied.

FAMILY HAMOPHTHIRIIDAE

Mjöberg (1925) described a rather peculiar new sucking louse, which he named *Hamophthirius galeopithecis* (fig. 122), from a flying lemur in British North Borneo. Ewing (1929) decided that Mjöberg's new genus was not closely related to other lice, so he placed it in a new subfamily, Hamophthiriinae, of the family Hoplopleuridae. Ferris (1951) did not recognize Ewing's new subfamily and left *Hamophthirius* in the subfamily Polyplacinae, which he had established. From 1925 to 1969, *Hamophthirius* was known only from Mjöberg's description because his type specimens were apparently lost. After receiving additional material from the flying lemur, *Cynocephalus variegatus* (Dermoptera: Cynocephalidae), Johnson (1969) elevated Ewing's subfamily to family rank and provided the following description for the monotypic family Hamophthiriidae. The description also applies to the genus and species.

Hamophthiriidae are Anoplura without external evidence of eyes. Both the head and basal segment of the antennae bear a strong posteriorly directed hook. The antenna is three-segmented, with the basal segment much larger than the two apical segments (fig. 122). The thoracic sternal plate is large, is rounded in front, and has two well-developed sternal processes extending backward. The posterior margin of the sternal plate is free from the thorax. Paratergal plates on abdominal segments 37 (fig. 123) are extended into short points. Male and female genitalia are illustrated in figure 124 (Johnson 1969).

The host of *Hamophthirius galeopithecis* is the flying lemur, which is believed to have descended from the same stock as the bats (order Chiroptera) (Simpson 1945), but bats are not parasitized by either Mallophaga or Anoplura. Because bats do have many other ectoparasites (including some specialized Diptera and Hemiptera), their lack of lice has puzzled entomologists for many years. For example, Hopkins (1949) stated that if *Hamophthirius galeopithecis* did not originate with the flying lemurs, then the absence of lice from bats is an acquired condition, not a primitive one.

FAMILY HOPLOPLEURIDAE

Ferris (1951) elevated Ewing's (1929) subfamily Hoplopeurinae to family rank and included five subfamilies and most of Ewing's species. In her review of the Hoplopleuridae of the Indo-Malayan subregion, Johnson (1964) removed *Pedicinus* but left Ferris' other subfamilies undisturbed. Kim and Ludwig (1978a) removed three of Ferris' subfamilies and the genus *Ratemia* from Hoplopleuridae and gave them family rank. The remainder of Hoplopleuridae were then either left in the typical subfamily with 2 genera and 122 species or placed in a new subfamily, Haematopinoidinae, with 3 genera and 10 species. The Haematopinoidinae parasitize moles (Insectivora: Talpidae and Soricidae) and myomorphic rodents (Rodentia: Gliridae) (dormice), while Hoplopleurinae parasitize rodents and lagomorphs.

Hoplopleuridae are small-to-medium sucking lice without external indication of eyes. The ocular points are not prominent, and the thorax does not have a notal pit or a sternal apophyseal pit. The legs differ in size, with hindlegs being the largest. The tibial claws of the hindlegs are highly developed.

Genus *Hoplopleura*

The genus *Hoplopleura* contains more species than any other genus of Anoplura; there are 136 according to Durden and Musser (1994b). A few species infest and injure laboratory animals and can make those animals unfit for use in research. The species of *Hoplopleura* are difficult to identify, and misidentifications have caused confusion about host relationships and geographical distribution (Johnson 1960, 1964).

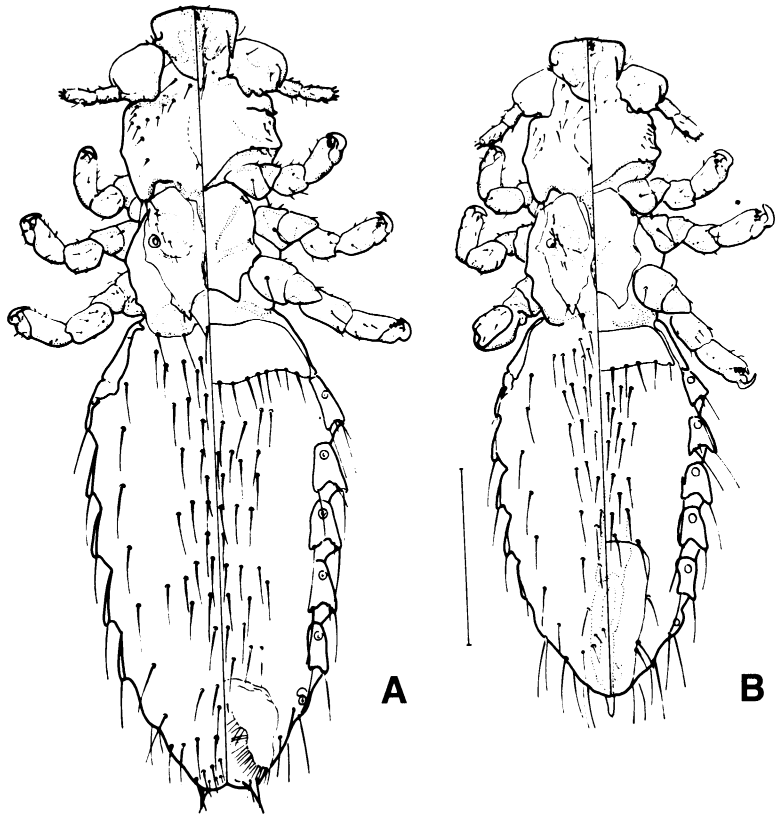


Figure 122. *Hamophthirius galeopitheci*: ***A***, Dorsoventral view of female; ***B***, dorsoventral view of male. From Johnson (1969), courtesy of Proceedings of Entomological Society of America.

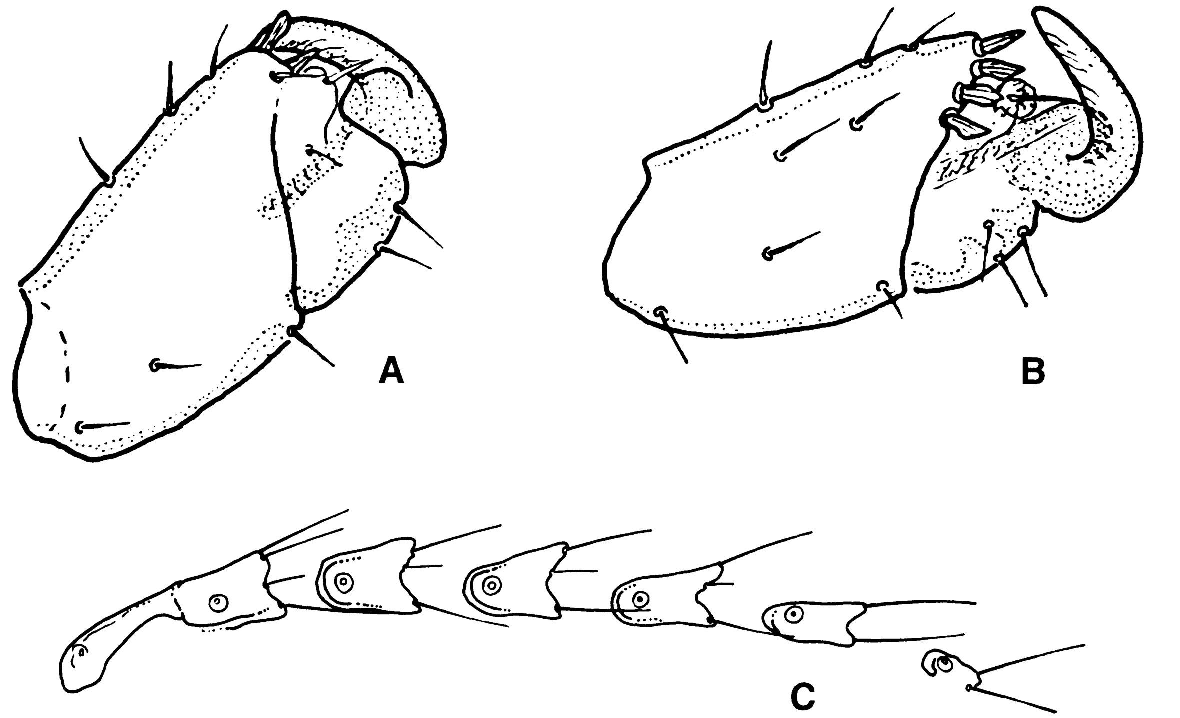


Figure 123. Taxonomic details of *Hamophthirius galeopitheci*. ***A***, Dorsal view of tibia, tarsus, tarsal claw of first leg, female; the claw and modified tibial setae form the tibial thumb; ***B***, same, except ventral view of third leg, male; ***C***, paratergal plates 2 to 8, female. From Johnson (1969), courtesy of Proceedings of Entomological Society of Washington.

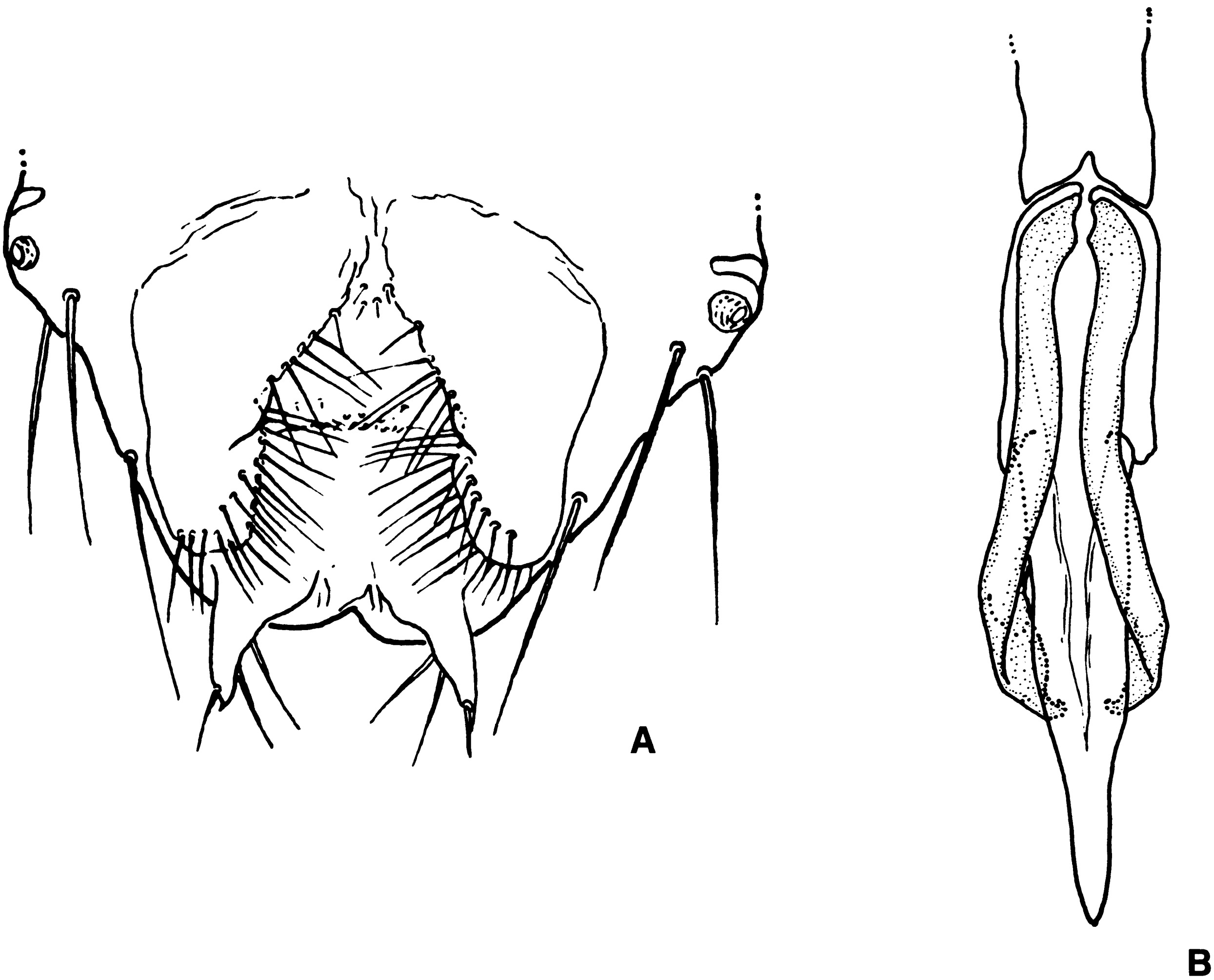


Figure 124. Taxonomic details of *Hamophthirius galeopitheci*. ***A***, Female terminalia; ***B***, male genitalia. From Johnson (1969), courtesy of Proceedings of Entomological Society of Washington.

The antennae of *Hoplopleura* are clearly five-segmented. The sternal plate of the second abdominal segment and usually the sternal plate of the third abdominal segment are extended laterally to articulate with the corresponding paratergites; these two plates are always narrow. The paratergites never show any indication of division into dorsal and ventral parts (Johnson 1960). The chorionic architecture of the eggs of six Neotropical species of *Hoplopleura* was described by Castro et al. (1991).

The injuries caused to laboratory animals by sucking lice are similar to those suffered by cattle. The animals lose hair by scratching, biting, and rubbing; in severe cases, they develop anemia and may die.

Hoplopleura acanthopus

The most common hosts of *Hoplopleura acanthopus* (fig. 125) are voles (*Microtus* spp.), but they are sometimes found on several wild mice and occasionally on the house mouse (*Mus musculus*) and the laboratory mouse (Ferris 1951, Kim et al. 1973). According to Parnas et al. (1960), the louse may be a carrier of *Brucella brucei* (probably =*Brucella neotomae*). Durden (1992) found the *Hoplopleura* to be host specific; he collected only *H. acanthopus* from meadow voles (*Microtus pennsylvanicus)* and only *H. hesperomydis* (fig. 126) from white-footed mice (*Peromyscus leucopus*).

Hoplopleura captiosa

While primarily a parasite of the house mouse, *Hoplopleura captiosa* is sometimes found on laboratory mice. The species, which was described by Johnson (1960), has been confused in the literature with *Hoplopleura hesperomydis* and *H. acanthopus*. It occurs in Asia, Europe, Africa, and the United States (California and Virginia) (Kim 1965).

Hoplopleura hirsuta

A parasite of the cotton rat (*Sigmodon hispidus*) in the southern United States, *Hoplopleura hirsuta* (fig. 127) has a distribution extending from Oklahoma and Texas to Virginia.

Hoplopleura imparata

Hoplopleura imparata has been collected from South American field mice (*Akodon* spp.) in Paraná State, Brazil (Barros et al. 1993).

Hoplopleura oryzomydis

It has sometimes been misidentified as *Hoplopleura pacifica,* but *H. oryzomydis* is the normal sucking louse of the rice rat (*Oryzomys palustris*) in North America (Durden 1988).

Hoplopleura pacifica

The tropical rat louse, *Hoplopleura pacifica*, was believed by Ferris (1951) to be a synonym of *Hoplopleura oenomydis*, but Johnson (1964) restored *H. pacifica* as a valid species. Johnson (1960) had earlier noted that Ferris' records of *H. oenomydis* from *Rattus calcis* and *Limnomys mearnsi* in the Philippines were actually records of *H. pacifica*. Johnson (1972) reviewed the taxonomy of *H. pacifica* and six closely related species. The Norway rat, black rat, and some wild rats are also hosts of *H. pacifica* in certain tropical areas, but Kim et al. (1973) could not find any reports of this louse from laboratory-raised rats. Roberts (1991a,b) found *H. pacifica* to be an ubiquitous parasite of the Polynesian rat, *Rattus exulans*, on some Pacific Islands. It also occurs on Madagascar, in Southeast Asia, southeastern United States, and the Caribbean Islands on the Norway rat. Durden (1990b) noted that the primary host for *H. oenomydis* is an East African murid, *Oenomys hypoxanthus*. *Hoplopleura pacifica,* as well as *Polyplax spinulosa,* is a capable vector of murine typhus from rat to rat (Durden and Page 1991).

Genus *Pterophthirus*

Although *Pterophthirus* is closely related to *Hoplopleura* (Ferris 1951), Kim and Ludwig (1978b) chose to separate them; they recognized five species of *Pterophthirus*. All are parasites of rodents in the family Cavidae (guinea pigs) or family Echimyidae (spiny rats) in South America and Panama.

Other Genera

Other genera of lice in the family Hoplopleuridae, but subfamily Haematopinoidinae, are the monotypic *Haematopinoides*, which parasitizes North American moles (*Scalopus aquaticus* and *Parascalopus breweri*; Insectivora: Talpidae); *Ancistroplax*, a parasite of shrews (Insectivora: Soricidae); and *Schizophthirus*, a parasite of dormice (*Gliridae*) and small rodents of the families Dipodidae and Myoxidae. Whitaker and French (1988) reported a low incidence of *Haematopinoides squamosus* from the hairy-tailed mole (*Parascalops breweri*).

FAMILY HYBOPHTHIRIDAE

Ferris (1951) placed two genera, *Hybophthirus* and *Scipio*, in the subfamily Hybophthirinae of his family Hoplopleuridae. These genera had previously been in Haematopinidae (Webb 1946), but because of the presence of a peculiar clawlike structure alongside the

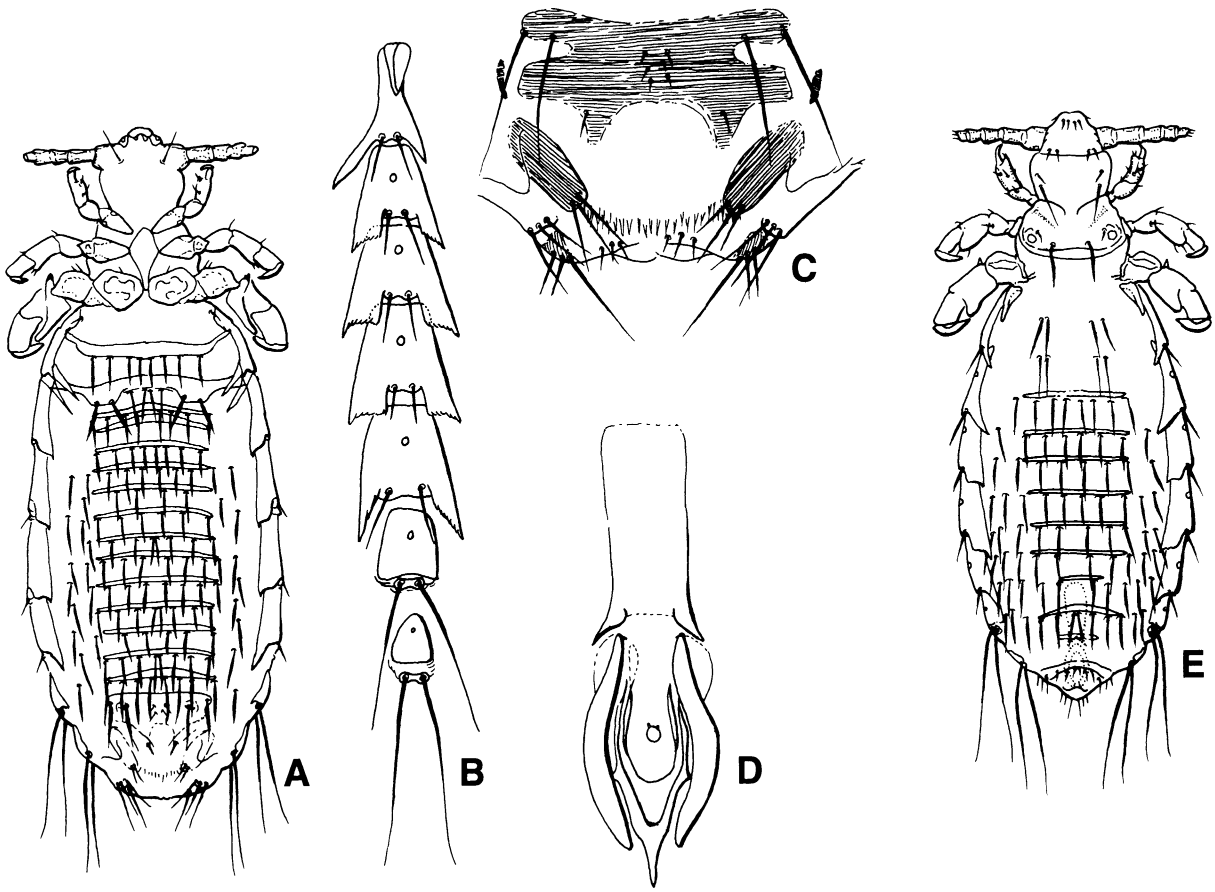


Figure 125. *Hoplopleura acanthopus*: ***A***, Ventral view of female; ***B***, paratergal plates; ***C***, female terminalia; ***D***, male genitalia; ***E***, dorsal view of male. Redrawn with minor modification by Jan Read from Ferris (1951); courtesy of Pacific Coast Entomological Society.

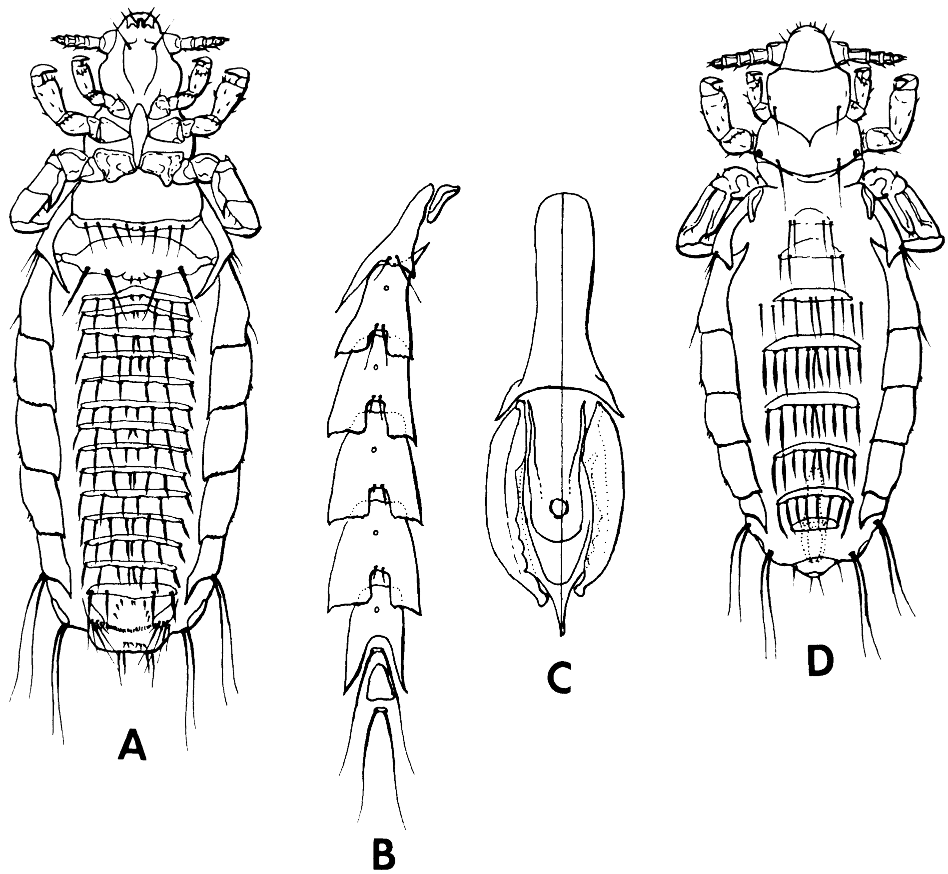


Figure 126. *Hoplopleura hesperomydis*: ***A***, Ventral view of female; ***B***, paratergal plates of female; ***C***, male genitalia; ***D***, dorsal view of male. Redrawn with minor modification by Jan Read from Ferris (1921), Contributions Toward a Monograph of the Sucking Lice, Part 2, courtesy of Stanford University Publications.

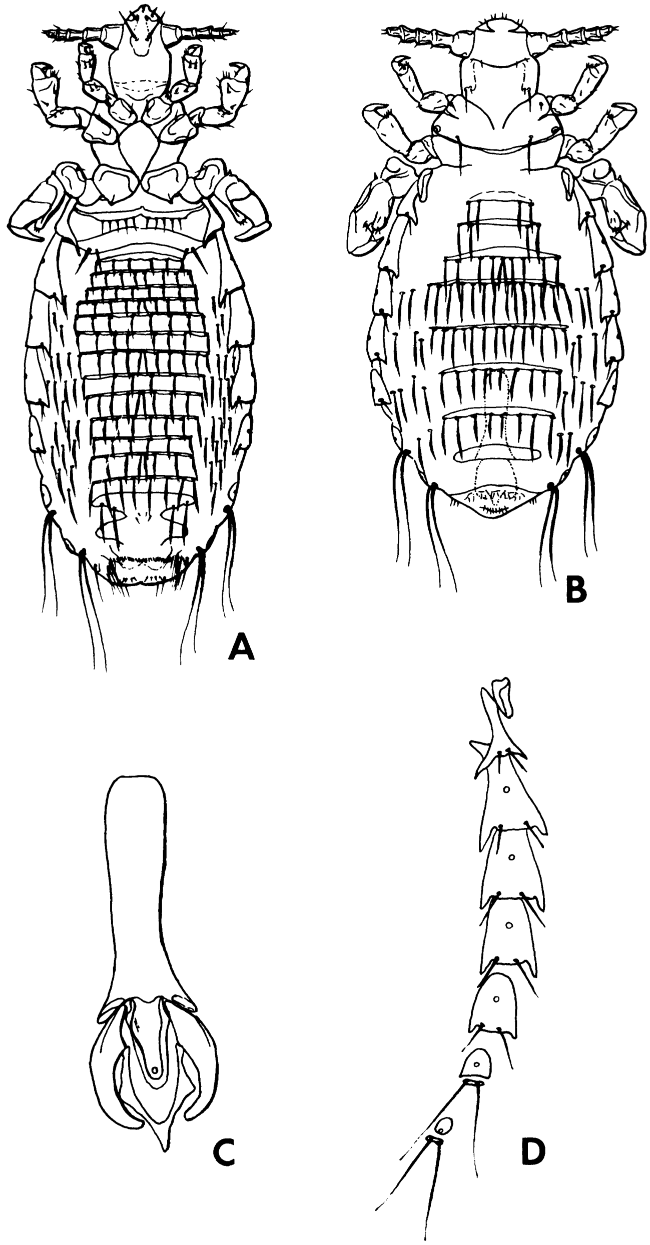


Figure 127. *Hoplopleura hirsuta*: ***A***, Ventral view of female; ***B***, dorsal view of male; ***C***, male genitalia; ***D***, pleural plates of female. Redrawn with minor modification by Jan Read from Ferris (1921), Contributions Toward a Monograph of the Sucking Lice, Part 2, courtesy of Stanford University Publications.

true claw on the front tarsus, Ferris established a separate subfamily to accommodate the genera. Kim and Ludwig (1978b) raised Ferris' subfamily to family rank but did not include *Scipio*, so the family Hybophthiridae now has only one species.

As the only species of Hybophthiridae, *Hybophthirus orycteropodis* (=*H. notophallus*) can be distinguished from other sucking lice by the presence of an additional clawlike structure at the base of the true claw (fig. 128), by the absence of a thoracic sternal plate, and by having the apex of the paratergites on abdominal segments 2–8 free from the body. *H. orycteropodis* is a parasite of aardvarks (Tubulidentata: Orycteropodidae).

FAMILY LINOGNATHIDAE

Enderlein (1905) described the genus *Linognathus* and subfamily Linognathinae and used the dog louse, *Linognathus setosus*, as the type species. Webb (1946) raised the subfamily to family rank. Ferris (1951) placed four genera in the family, but one was *Microthoracius*, about whose classification Ferris was uncertain. Kim and Ludwig (1978b) placed *Microthoracius* in its own family and thus left three genera in Linognathidae: *Linognathus*, *Solenopotes*, and *Prolinognathus*.

The head of Linognathidae is without external evidence of eyes. The thorax has well-developed mesothoracic and metathoracic phragmata as well as distinct or occasionally obscure notal pits. The forelegs are the smallest; midlegs are subequal to hindlegs or at least somewhat larger than the forelegs. Each leg has a large, stout claw. The abdomen is membranous, with no trace of sternal or tergal plates except for those associated with genital and terminal segments. The paratergites are absent or at most represented by small tubercules anterior to each spiracle (Kim et al. 1986).

Hosts are in the orders Artiodactyla (families Bovidae, Cervidae, and Giraffidae), Perissodactyla (family Equidae), Carnivora (family Canidae), and Hyracoidea (family Procaviidae).

Genus *Linognathus*

As recognized by Kim and Ludwig (1978b), the genus *Linognathus* contains 51 species—more than any other genus of Linognathidae. The species parasitize mammals in the orders Artiodactyla and Carnivora. Ferris (1951) described the genus as follows: The species of *Linognathus* can be recognized by their five-segmented antennae and by not having a thoracic sternal plate; or if present, the plate is weakly developed and may be divided longitudinally into two small plates. The abdominal spiracles are more or less spherical and are not reduced in size. The abdominal segments have abundant setae both dorsally and ventrally, usually arranged in at least two transverse rows.

Linognathus africanus

In the South African literature, *Linognathus africanus* (fig. 129) is referred to as the African blue louse or just the blue louse, and some American authors have used the same common name. The species is recognized by its greatly expanded postantennal lateral margins (fig. 130) and very slender thoracic sternal plate. The genital region of both sexes is also distinctive; the gonopods of segment 8 of the females are elongated and rounded at the extreme apex (fig. 131). Females are 2.15 mm long and males 1.65 mm. O'Callaghan et al. (1989) described the separation of *L. africanus* from *Linognathus stenopsis*; an important characteristic of *L. africanus* is the bulging posterolateral margins of the head (fig. 132). Other characteristics are shown in SEM's in figures 132–135.

Some reports of the goat sucking louse, *Linognatus stenopsis*, should have referred to *L. africanus*. Despite definite morphological differences, the two species are similar in size, and *L. africanus* can be misidentified under field conditions. Roberts (1952), in what appears to be an error, listed *L. africanus* as a synonym of *L. stenopsis*.

L. africanus was originally described from sheep in southern Nigeria (Kellogg and Paine 1911). Since then, it has been reported from the southern and southwestern United States (Kim et al. 1986), Puerto Rico (Van Volkenberg 1936), Hawaii, the Philippines, India (Rao et al. 1977), Africa (Ferris 1951), Libya (Gabaj et al. 1993), Spain (Portus et al. 1977), Palau (Belau) and the Mariana Islands (Wilson 1972), and Australia (O'Callaghan et al. 1989).

Life history. The egg of *Linognathus africanus* may be attached to a single hair on the host, but many times the female louse pulls several hairs together and attaches its egg to all. The latter behavior accounts for the matting of hairs or wool that is sometimes seen in heavily infested goats or sheep (Babcock and Cushing 1942c). The incubation period varies from 7 to 14 days, depending on air temperature and other factors. Baker (1969) stated that, in South Africa, the longest hatching period for eggs held in vitro was 8 days.

Host-parasite relationships and economic importance. Sheep and goats are the normal hosts of *Linognathus africanus*. Menzies et al. (1951) found that the louse was abundant on goats in Texas. Rao et al. (1977) reported it from both goats and cattle at Mandya, India. In addition, Brunetti and Cribbs (1971) reported it from California mule deer (*Odocoileus hemionus californicus*) and

Figure 128. Front tarsus of *Hybophthirus orycteropodis.* Note small secondary claw (at arrow) on side of true claw. From Kim and Ludwig (1978a), reprinted by permission of Blackwell Science Ltd, Oxford, United Kingdom.

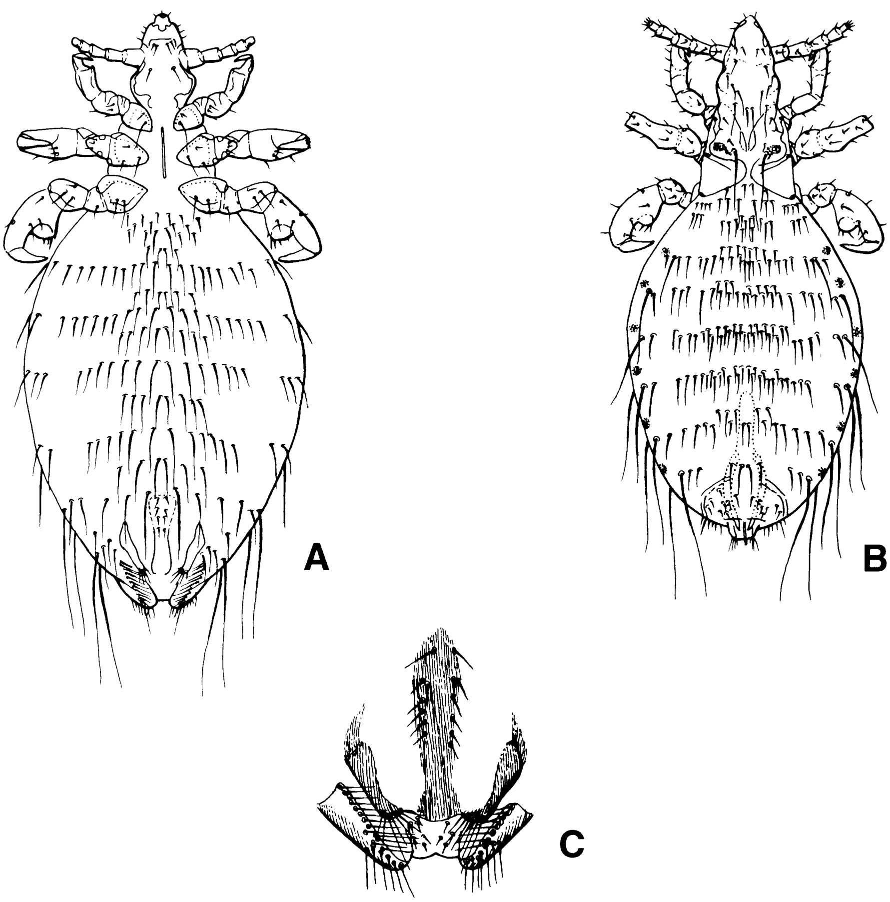


Figure 129. *Linognathus africanus*: ***A***, Ventral view of female; ***B***, dorsal view of male. Redrawn with minor modification by Jan Read from Ferris (1951); courtesy of Pacific Coast Entomological Society.

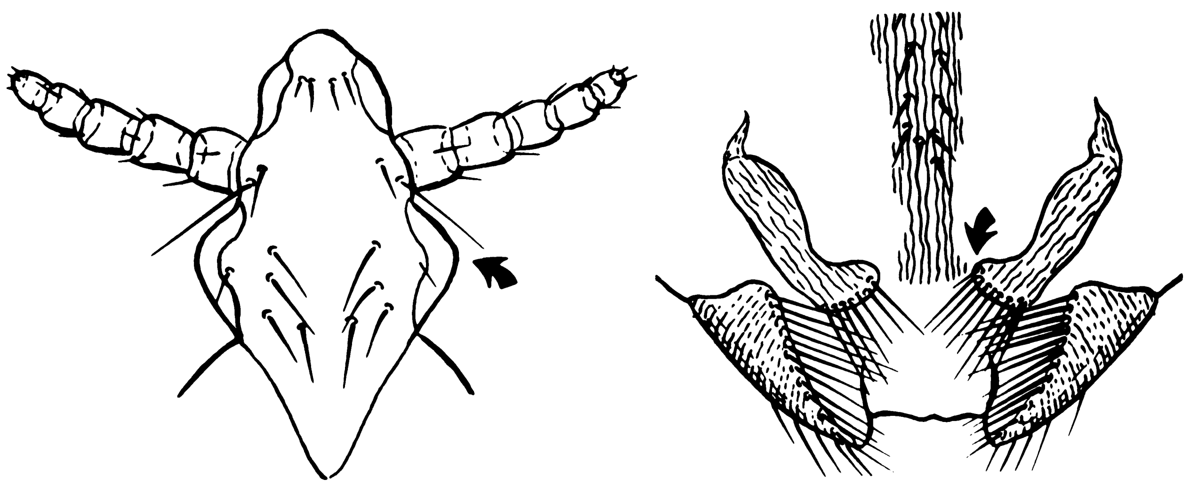


Figure 130. Recognition of *Linognathus africanus*. Note expanded postantennal margins of head (left arrow) and rounded female gonopod (right arrow). From Stojanovich and Pratt (1965), Key to Anoplura of North America, U.S. Department of Health, Education, and Welfare.

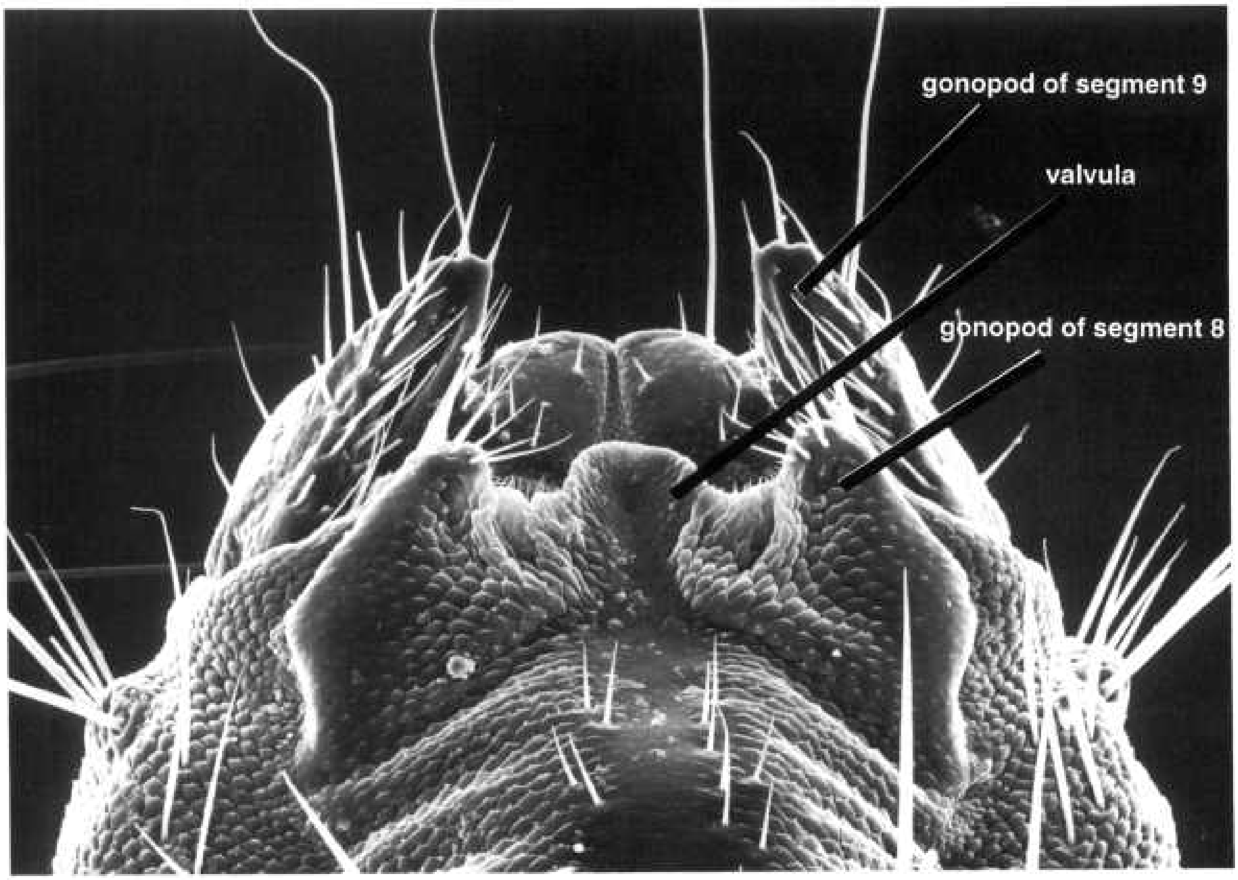


Figure 131. *Linognathus africanus*: Ventral view of female terminalia. SEM × 150, by Theresa Droste; courtesy of Department of Entomology, Texas A&M University.

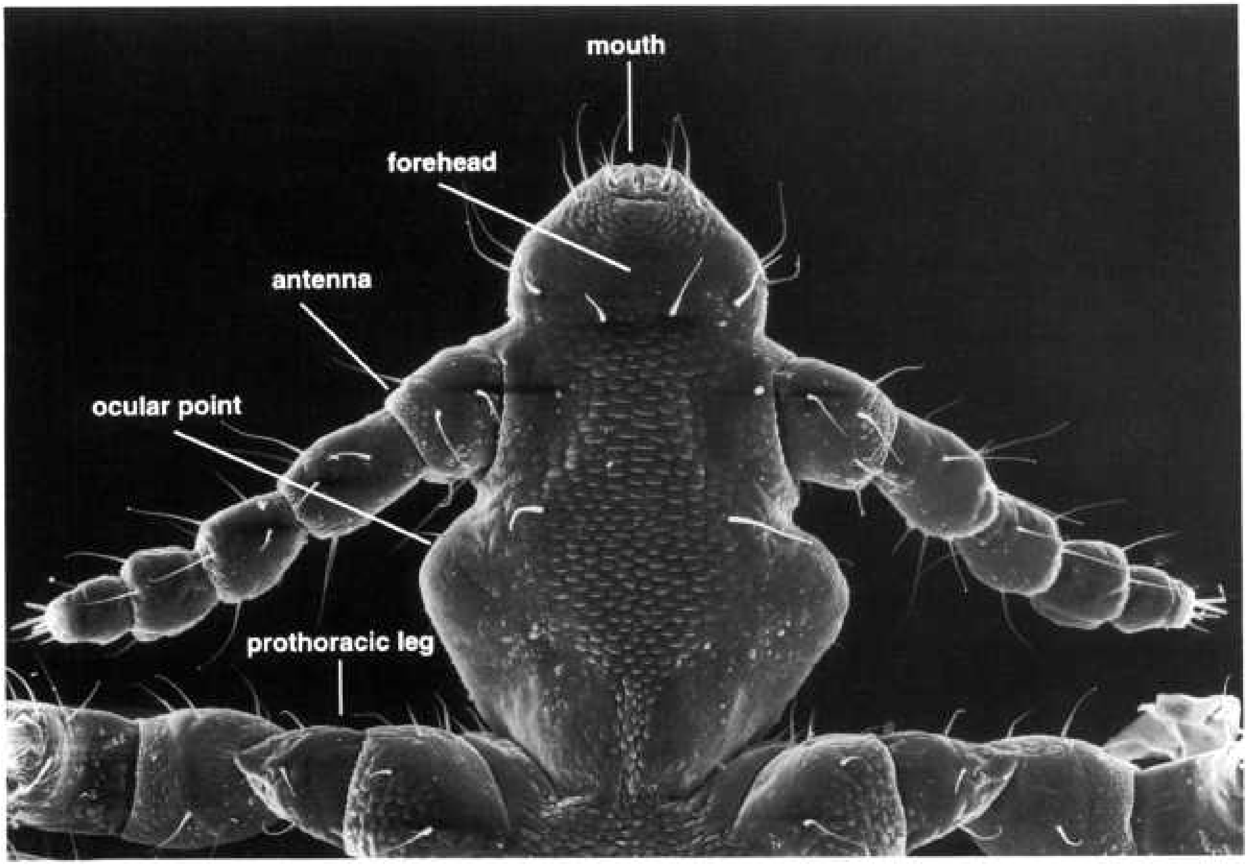


Figure 132. *Linognathus africanus*: Ventral view of head. SEM × 110, by Theresa Droste; courtesy of Department of Entomology, Texas A&M University.

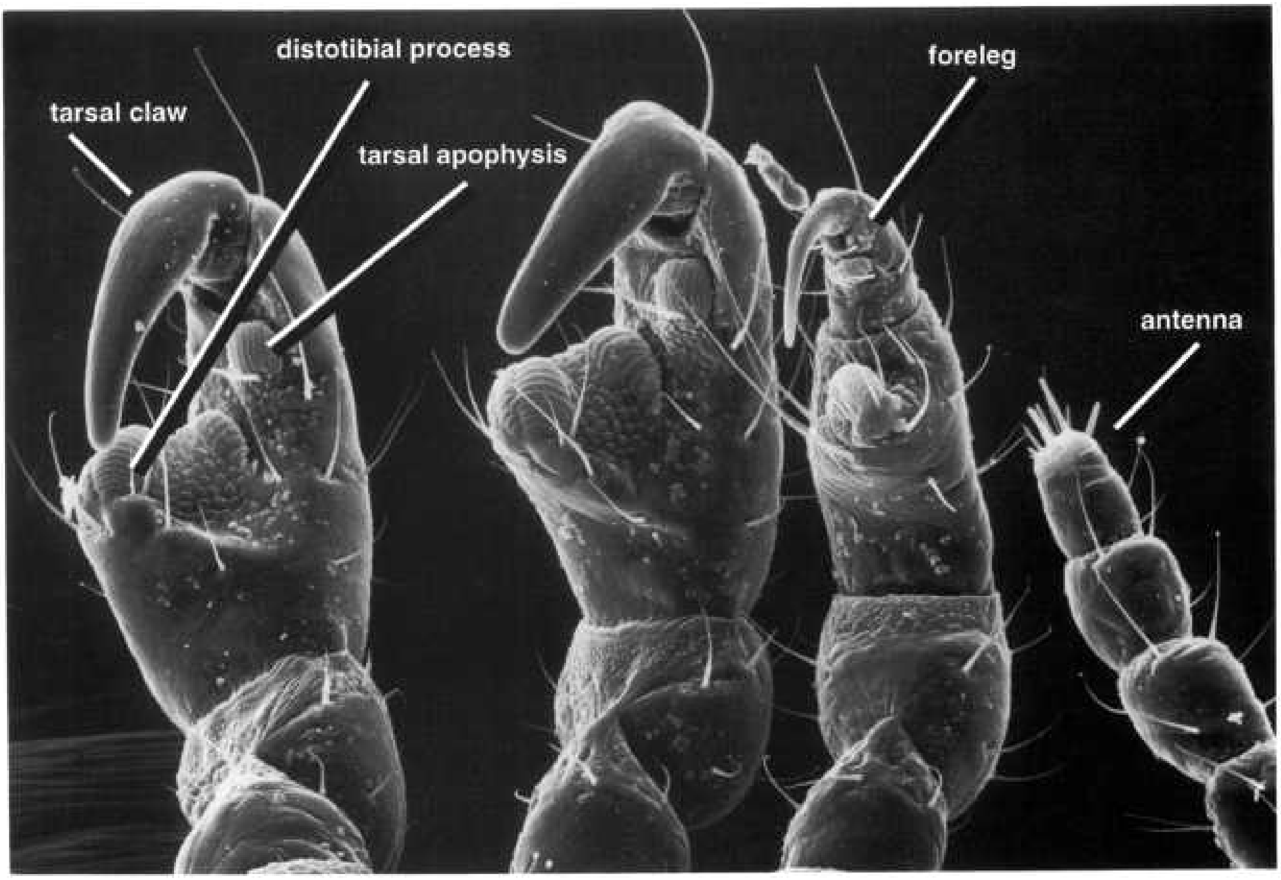


Figure 133. *Linognathus africanus*: Ventral view of tarsi. Note that tarsal claws on midlegs and hindlegs are much larger than those on forelegs. SEM × 150, by Theresa Droste; courtesy of Department of Entomology, Texas A&M University.

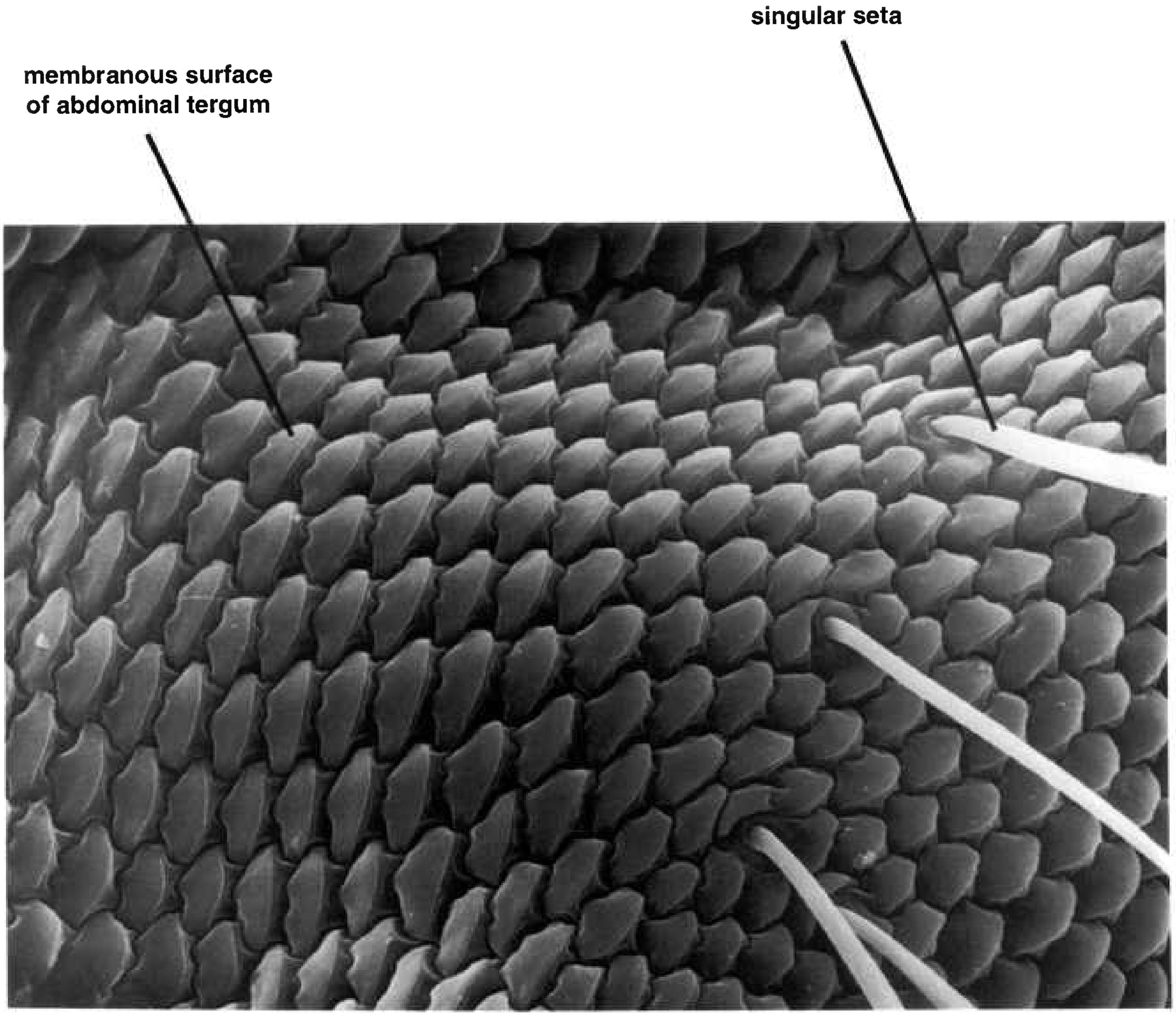


Figure 134. *Linognathus africanus*: Surface of the tergum at midabdomen. SEM × 570, by Theresa Droste; courtesy of Department of Entomology, Texas A&M University.

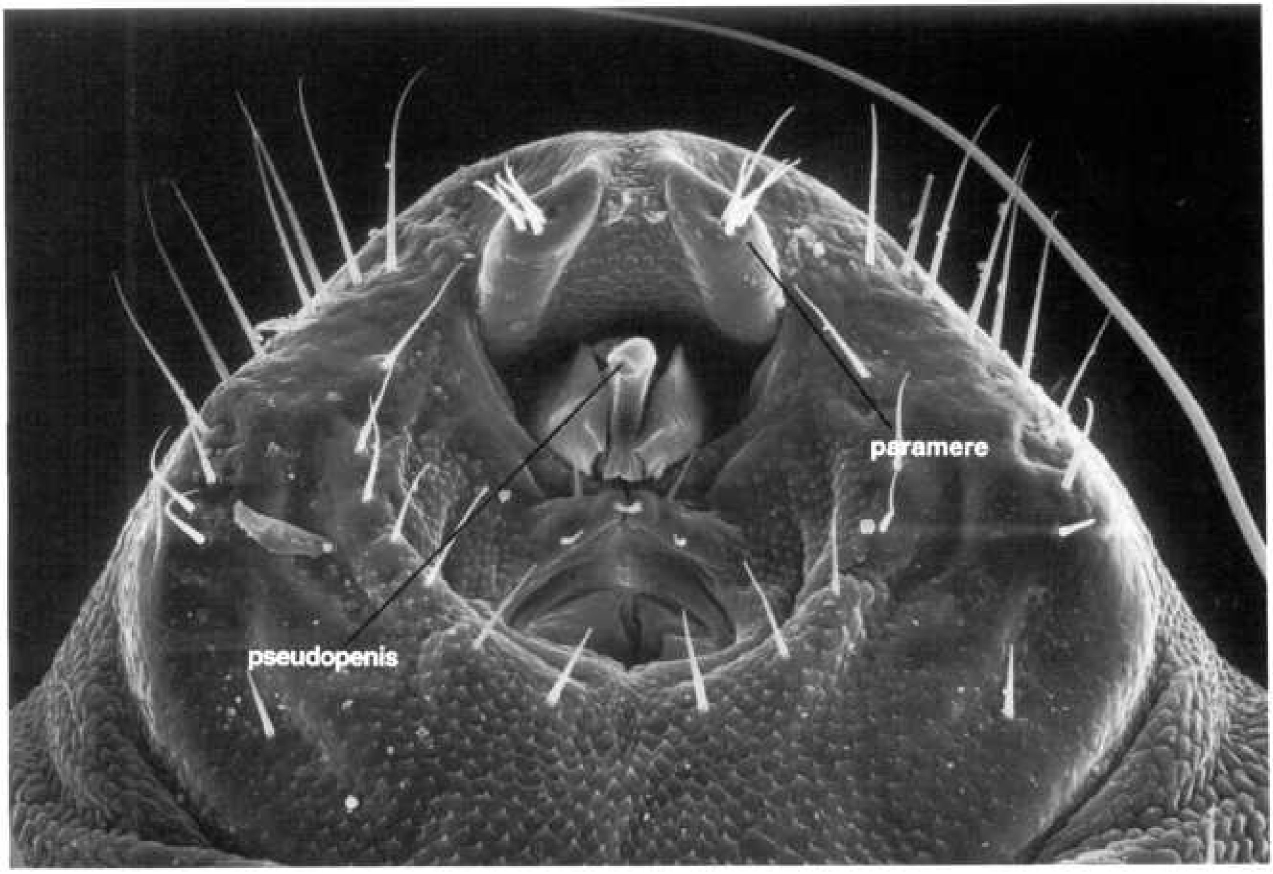


Figure 135. *Linognathus africanus*: Ventral view of male genitalia. SEM × 120, by Theresa Droste; courtesy of Department of Entomology, Texas A&M University.

Columbian black-tailed deer (*Odocoileus hemionus columbianus*). It has also been recovered from white-tailed deer (*Odocoileus virginianus*) and a purported subspecies of *L. africanus* from gazelles (*Gazella granti*) in Africa (Kim et al. 1986). Lozoya-Saldaña et al. (1986) mentioned that goats were the principal host of *L. africanus* in northern Mexico, but they also collected stragglers from cattle, a dog, and a turkey.

The injuries to sheep that are caused by *L. africanus* were described by Kemper and Hindman (1950). It was their observation that more than half of the coarse-wooled Hampshire and Suffolk rams were lightly to heavily infested, whereas they could not find lice on any of the fine-wooled Rambouillet rams in the same flock. Heavily infested sheep had bare spots along the sides of their bodies where they had rubbed themselves against fences and posts to relieve itching (fig. 136). Sometimes the wool slips from skin areas either as a direct result of lice being present or, more likely, as the result of a fever produced (at least in part) by the lice. They found most of the lice along the sides of the sheep, especially over the ribs. But in South Africa, Baker (1969) reported that Angora goats with only a few lice were most likely to have them on the upper neck, base of the ears, poll, and ventral surface of the jaw. Thorold (1963) stated that massive infestations of *L. africanus* may produce anemia with edema of the legs and underline in goats and, if not controlled, may cause death of the animal—particularly kids. Like sheep, Angora goats suffer severe skin irritation, causing them to scratch and rub and thus damage their valuable hair coat.

Deer also suffer if severely infested with *L. africanus*. Brunetti and Cribbs (1971) investigated a report from Kern County, California, where a number of mule deer had died at least in part from louse attacks. A 16-kg fawn, which had died from exsanguination anemia, was estimated to have been parasitized by 1.52 million blue lice. Other deer carcasses were similarly infested. The deaths occurred mainly in December and January during heavy snowfalls; the authors concluded that louse infestation, in combination with other stress factors, was the cause of death. Deer die-off from other areas of California caused by anemia following massive infestations of *L. africanus* was noted by Brunetti and Cribbs.

Linognathus ovillus

In the Australian and other literature, *Linognathus ovillus* is referred to as the face louse of sheep. It is distinguished by a head that is broad but fully twice as long as wide (Ferris 1951). If present, the thoracic sternal plate is narrow and slender (Kim et al. 1986). It has normal (not short), stout, fusiform abdominal setae (fig. 137). The female gonopods are rather small and rounded posteriorly; the male genitalia have parameres that are slender and curve inwardly at the apex. The female abdomen is covered with setae on the dorsal surface that are arranged in rows, with longitudinal bare areas between the rows (Roberts 1952). The female averages 2.25 mm long and the male 2.0 mm.

Linognathus ovillus was originally described by Neumann (1907) from domestic sheep in Scotland and New Zealand (Ferris 1951, Murray 1955a). It has also been reported from the United States, Russia, the Falkland Islands, and Australia, although not verified from the United States (Kim et al. 1986). Murray listed records of *L. ovillus* from Australia, but at the same time pointed out that some observers had confused *L. ovillus* with *Linognathus pedalis*.

Life history. The ovipositional behavior of female *Linognathus ovillus* is similar to that of other lice on sheep and goats (Murray 1955a, 1963a,b). The louse moves to the warm end of the hair or wool fiber, rests a short time, then reverses its position on the hair, grasps a hair with its gonopods, and lays an egg. The female readily attaches its egg to either coarse or fine fibers and to either hair or a wool fiber. If the louse is in a temperature gradient of 20–40 °C, it selects the warm end of the gradient for oviposition; most eggs are deposited at about 35 °C. Within the range of 33%–100%, relative humidity does not seem to influence oviposition. Females laid about one egg per day.

Incubation proceeds normally on either natural or artificial fibers. Almost all eggs held at 35 °C and 37 °C hatched, although emergence was negligible from eggs held at those temperatures and at 92% or 100% relative humidity. At 37.5 °C, eggs hatch in 11–13 days; at 32 °C, they hatch in 13–16 days (Murray 1955a). A complete life cycle, egg to egg, was completed in about 5 wk.

Murray (1963b) found no evidence to indicate that *L. ovillus* reproduces parthenogenetically.

Host-parasite relationships and economic importance. Domestic sheep are both the type and normal host for *Linognathus ovillus* (Ferris 1951, Kim et al. 1986).

The face louse is usually found on hairy parts of the sheep's face, especially in the hair on the cheeks and in the edge of the wool surrounding the hairy parts of the face (Murray 1963a). As louse populations increase in winter, they also spread to other parts of the body; by spring, heavily infested sheep have lice on all parts of their body. However, these lice do not form dense clusters of adults, nymphs, and eggs at various sites on the body as do some other species of lice.

Figure 136. Severe infestation of *Linognathus africanus* has caused the wool to slip from side of abdomen of this sheep. Courtesy of Dr. John E. Lloyd, University of Wyoming.

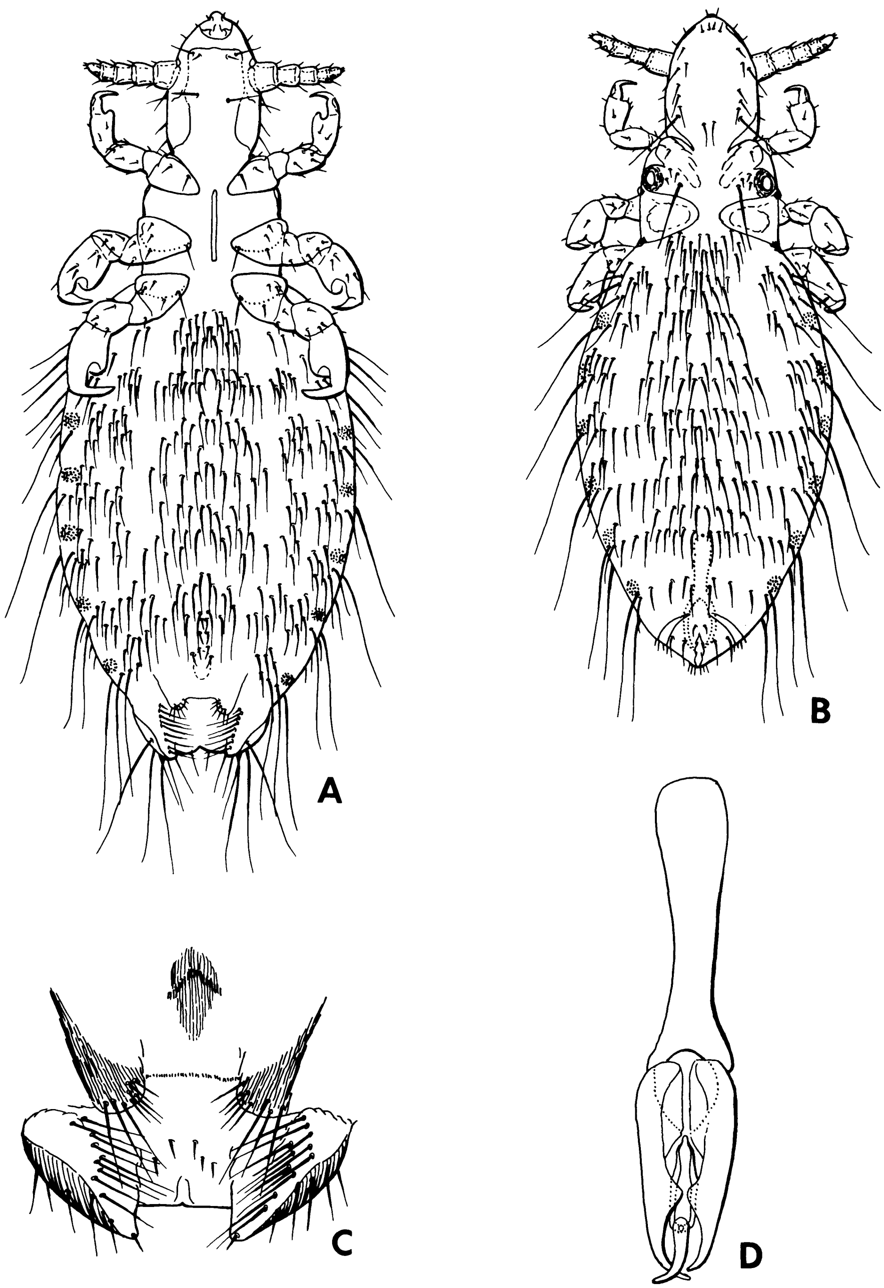


Figure 137. *Linognathus ovillus*: ***A***, Ventral view of female; ***B***, dorsal view of male; ***C***, female terminalia; ***D***, male genitalia. Redrawn with minor modification by Jan Read from Ferris (1951); courtesy of Pacific Coast Entomological Society.

Many lice are removed from infested sheep when they are sheared. Other lice are killed by high temperatures of the fleece, 47–48 °C and above, during summer. At least in part, reduced populations in summer are accounted for by these two factors.

Roberts (1952) and Butler (1986) agreed that *L. ovillus* is rare and economically unimportant in Australia, which is apparently true for Queensland, where Roberts worked. But face lice are not rare in Tasmania; Butler found them in all districts, including Flinders Island. Also, Murray (1955a) described a flock in Victoria that was so heavily infested that fleeces of the more severely infested sheep were stained by lice and their excreta; as a result, the market value of the wool was reduced. In addition, shearers were reluctant to handle sheep with so many lice. Apparently the louse seldom harms sheep.

Linognathus pedalis

True to its common name, the foot louse of sheep (*Linognathus pedalis*) ordinarily exists at a low population level on hairy parts of the sheep's foot and seldom invades the body areas that are covered with wool. This louse is distinguished by a small, short head (fig. 138) that is about as broad as long. The thoracic sternal plate is absent. The mesothoracic and metathoracic phragmata are disconnected. One long seta arises from small thoracic spiracles on each side of the dorsum of the thorax. The thoracic and abdominal spiracles are not strikingly large as in *Linognathus setosus*. The abdominal setae are long, slender, and numerous, and they are not arranged in discernable rows. Male and female genitalia are as shown in fig. 139. The female averages 2.07 mm long and the male 1.73 mm (Ferris 1951, Roberts 1952, Kim et al. 1986).

The foot louse is present in small numbers wherever sheep are raised. Scott (1950) stated that it has been recorded from every state in Australia, including Tasmania. It has also been reported from North America, South America, South Africa, New Zealand, and Great Britain, according to Roberts (1952), who added that it extends farther into the drier parts of Australia than do other sheep lice. Ansari (1951) listed Punjab, Rao et al. (1977) included India, and Gabaj et al. (1993) placed Libya in the area of foot louse occurrence.

Life history. When females of *Linognathus pedalis* were allowed to oviposit along a 20–40 °C temperature gradient, they selected the zone of 35–39 °C and laid the most eggs at 36 °C. All but five eggs were placed with the attached end pointing toward the warm end of the gradient. When the device was maintained at a uniform 36 °C throughout its le ʒth, the eggs were deposited randomly and with tne attached end pointing in either direction. Apparently relative humidity in the range of 33%–92% had little if any influence on choice of an oviposition site, but 100% relative humidity inhibited oviposition at 36 °C, the most favorable temperature for egg laying (Murray 1960a).

Scott (1950) found that on a lamb the minimum incubation period was 17 days. In the laboratory, Murray (1960a) found that the range of temperatures at which the eggs hatch was very narrow (33–38 °C) and that 36 °C and 54% relative humidity were optimum. Scott recorded incubation periods of 13–14 days at a constant 35 °C and 12–13 days at 36.5 °C. Murray did not observe any embryonic development or hatch in about 50% of eggs held at a combination of 36 °C and 92% relative humidity. It appeared that the lowest humidity tested by Murray, 33% relative humidity, was a favorable condition for hatching.

From studies by Scott in 1950 in which lambs were used as hosts, it appears that the period of development for each nymphal instar is 7 days or a total of 21 days. She found the preoviposition period to be 5 days, so the period of development from egg to egg for *L. pedalis* under her working conditions was 43 days. Scott also observed that females produce eggs at the approximate rate of one per day. In New South Wales, the natural population of *L. pedalis* reached its peak in August (winter) and its lowest point in January–May (summer to early fall).

Host-parasite relationships and economic importance. Domestic sheep are both the type and normal host for *Linognathus pedalis* (Ferris 1951, Kim et al. 1986). In addition, the mountain goat (*Oreamnos americanus)* has been reported as a host in the high altitudes of the northwestern United States and adjacent regions in Canada.

Scott (1950) found that if a sheep is lightly infested, these lice are most often seen between and around the dewclaws; but as the infestation becomes heavier, foot lice spread up the leg and around the hoof, and many lice and their eggs can be found on the hairy parts of the lower leg. This species does not normally invade the wool, but heavily infested sheep frequently have foot lice on the scrotum and hairy parts of the flanks, lower abdomen, brisket, and escutcheon. Scott noted that sheep with lice in summer tend to become heavily infested in winter, while those with few or no lice in fall tend to continue with very few lice year-round; this suggests some type of innate resistance in lightly infested animals.

Scott (1950) was particularly interested in the transmission of lice from one sheep to another and from infested premises to louse-free sheep. In her studies, a lamb

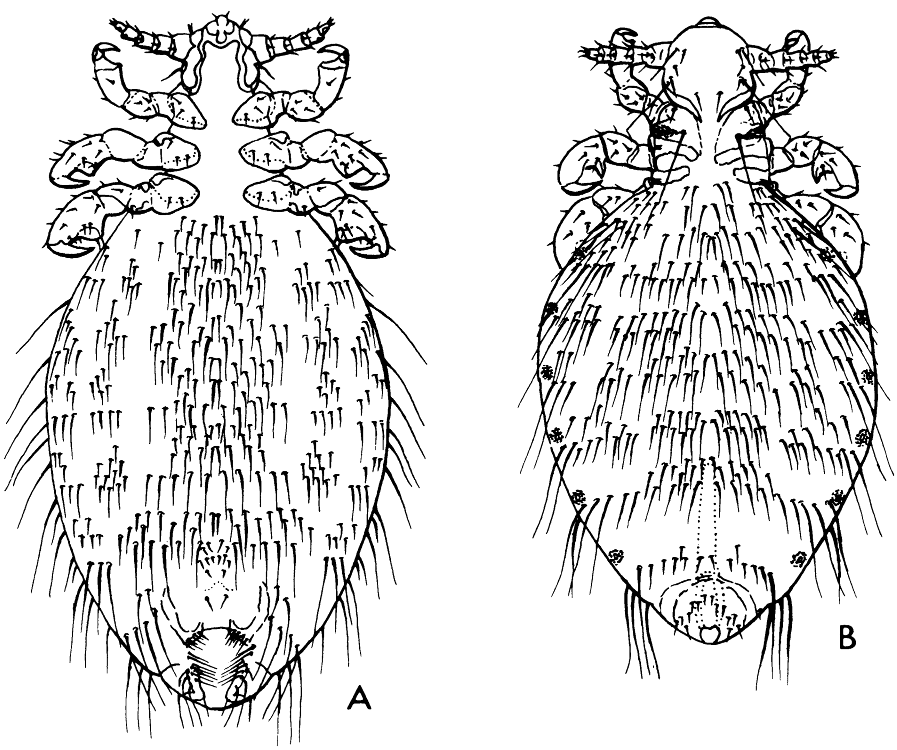


Figure 138. *Linognathus pedalis*: ***A***, Ventral view of female; ***B***, dorsal view of male. Redrawn with minor modification by Jan Read from Ferris (1951); courtesy of Pacific Coast Entomological Society.

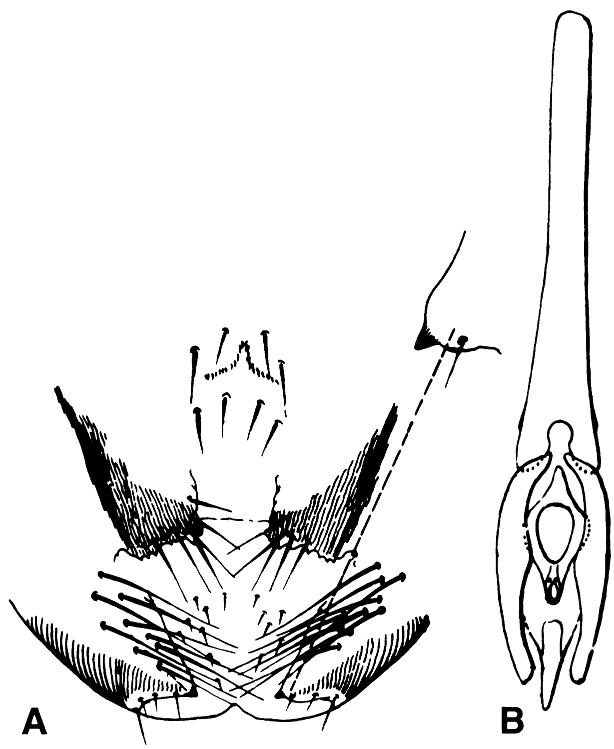


Figure 139. *Linognathus pedalis*: ***A***, Female terminalia; ***B***, male genitalia. From Ferris (1951), The Sucking Lice, courtesy of Pacific Coast Entomological Society.

became infested before it was 24 hr old, and a group of lambs were all infested before they were 3 mo old. She observed that lambs frequently became infested at an early age even though their dams carried few or no lice. Lambs became infested with *L. pedalis* when placed in infested premises within 48 hr (but not 72 hr) after the removal of infested sheep. Premise temperature was also a factor; Scott found that lice off a host could survive for only 3–5 days at 30–37 °C, but at 18–20 °C or 0–4 °C the maximum survival time was 18 days. Lambs also acquired lice from deliberately contaminated premises at 0, 24, and 48 hr after lice were placed on small, grassed areas where minimum to maximum temperatures of −3° to 20 °C were recorded.

As far as we are able to determine, massive infestations of *L. pedalis* are seen on only a few susceptible individuals in a flock. Injury caused by massive infestations of the foot louse are most apt to occur in rams—especially rams that are confined to stalls. Irritation makes those animals stamp their feet, kick, lose weight, and sometimes become lame (Roberts 1952, Price et al. 1967a).

Linognathus setosus **(dog sucking louse)**

Although it superficially resembles *Linognathus pedalis*, *L. setosus* (fig. 140) can be distinguished by the strongly sclerotized transverse bands across the front of its head and by having two long setae on each side of the dorsum of the thorax. Its head is slightly longer than broad, and the preantennal region is broader than long. The prothorax has two short setae on each side. The thoracic stigmal plate is missing, and the thoracic and abdominal spiracles are conspicuously large. The abdomen is oval. Male and female genitalia are as shown in figure 140. Females average 2.05 mm long and males 1.75 mm (Kim et al. 1986).

L. setosus is found on domestic dogs worldwide, but its incidence is probably low (Pennington and Phelps 1969). However, Koutz (1944) mentioned that it was very common in Ohio.

Life history. The eggs (fig. 141) of *Linognathus setosus* are deposited on host hair and hatch in 5–12 days. No other information is available about its life history (Kim et al. 1973).

Host-parasite relationships and economic importance. The domestic dog is both type and normal host of *Linognathus setosus*. Ferris (1951) also listed the Arctic fox (*Alopex lagopus*), "fox" from Manchuria, wolf (*Canis lupus*), Indian jackal (*Canis aureus*), black-backed jackal (*Canis mesomelas*), coyote (*Canis latrans*), red fox (*Vulpes fulva*), Old World red fox (*Vulpes vulpes*), ferret, and rabbit (the last two records are probably temporary transfers). *L. setosus* (=*L. piliferus*) is common on Arctic or blue foxes on islands off the coast of Alaska and is occasionally seen on ranch-reared foxes where it has a tendency to localize around the eyes, especially on the upper eyelids (Hanson 1932). Calaby (1970) added the dingo (*Canis dingo*) as a host in Australia. Menzies (1949) recorded *L. setosus* from the house mouse (*Mus musculus*), where it was probably a straggler.

The occasional heavily infested dog (Ewing 1929) is most apt to be one of the long-haired breeds that has been neglected. Heavy infestations of the dog sucking louse may cause severe irritation, debilitation, anemia, and weakness (Sosna and Medleau 1992a). The host is restless and scratches frequently; as a result, the skin becomes inflamed and patches of hair are lost.

In one instance, we saw a family pet with so many lice that the dog died, presumably from exsanguination anemia. Bezukladnikova (1960) stated that *L. setosus* may be found in large numbers on dogs, especially sickly dogs, in Kazakhstan, of the former USSR.

Linognathus stenopsis **(goat sucking louse)**

Although *Linognathus stenopsis* (fig. 142) has been confused with *L. africanus*, it can be separated by the presence of a small but distinct tooth on the apex of the female gonopod (fig. 143). The postantennal lateral margins of the head are not expanded, and the thoracic spiracle is not large and conspicuous. The thoracic sternal plate is very small and narrow. Female terminalia are as shown in figure 143. Females average 2.75 mm long and males 2.2 mm (Stojanovich and Pratt 1965, Kim et al. 1986).

The goat sucking louse is found worldwide but is most abundant in temperate zones (Kim et al. 1986).

Life history. Oviposition by *Linognathus stenopsis* has been described by Murray (1957a). On a temperature gradient, the behavior of female lice was very similar to that of *Linognathus ovillus* and *L. pedalis*. Murray noted that fully engorged females deposited two eggs per day for 2 days before they needed to feed again. Apparently other details of the life history have not been reported.

Host-parasite relationships and economic importance. The domestic goat is both the type and normal host for *Linognathus stenopsis* and has been reported from both short-haired and Angora breeds. In addition, it has been collected from sheep in Asia, Africa, and North America (Roberts 1952). By placing *Haematopinus forficulus* and *H. rupicaprae* in synonymy with *L. stenopsis*, Ferris (1951) added their hosts [the ibex (*Capra ibex*) and the chamois (*Rupicapra rupicapra*)] to the host list for *L. stenopsis*.

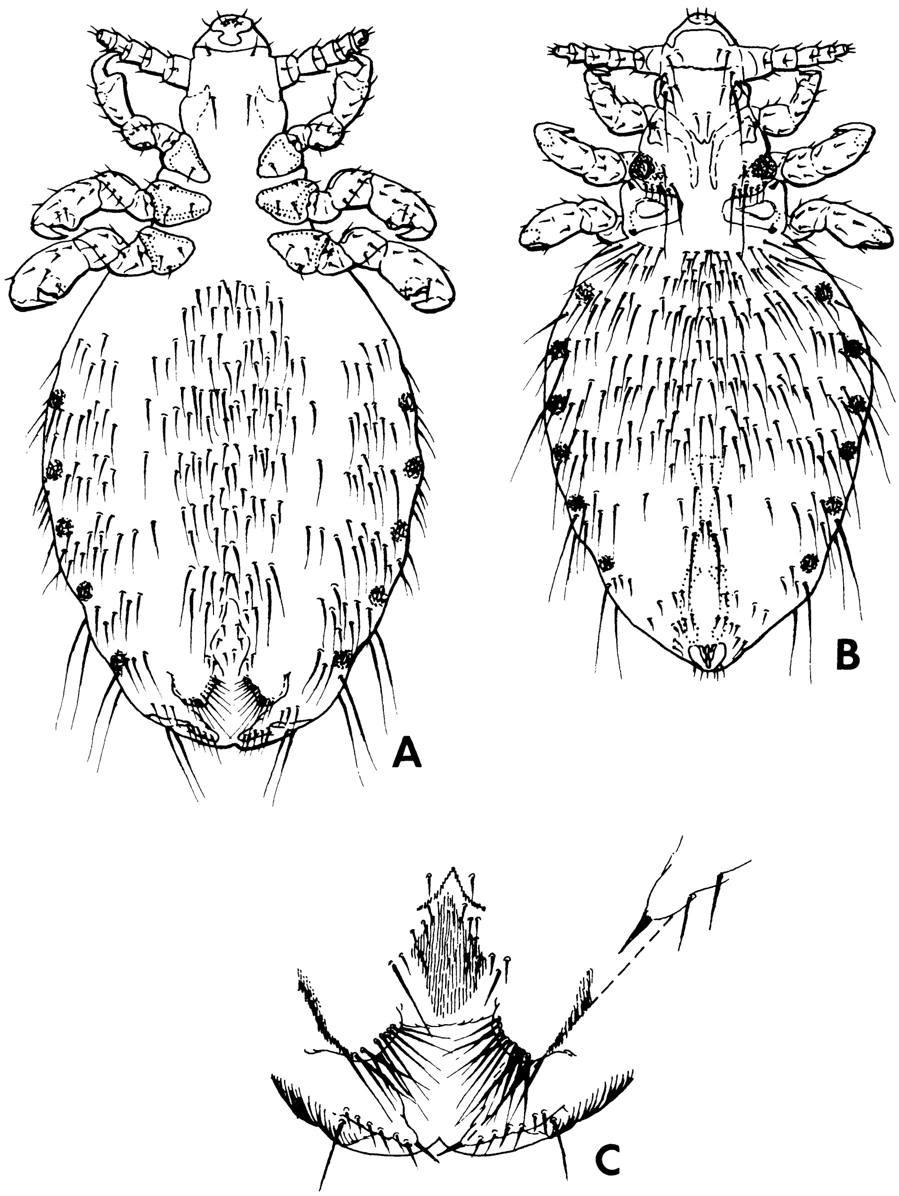


Figure 140. *Linognathus setosus* (dog sucking louse): ***A***, Ventral view of female; ***B***, dorsal view of male; **C**, female terminalia. Redrawn with minor modification by Jan Read from Ferris (1951); courtesy of Pacific Coast Entomological Society.

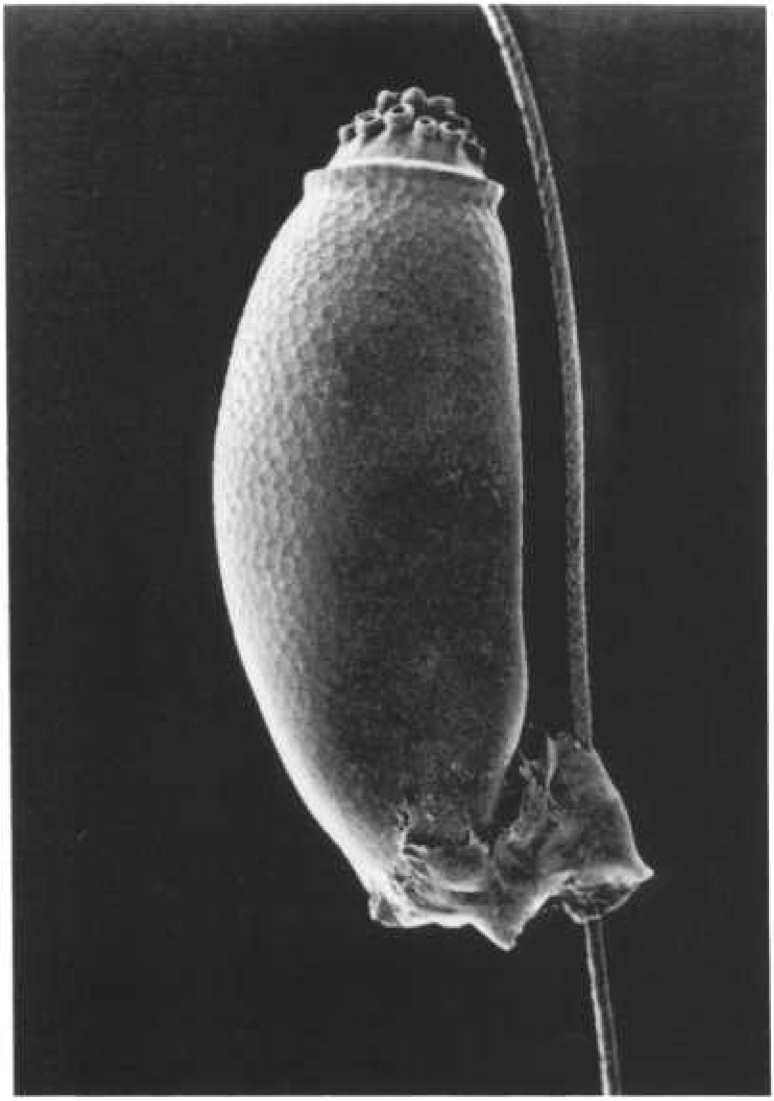


Figure 141. Egg of *Linognathus setosus*. SEM × 125, by Shirley Meola.

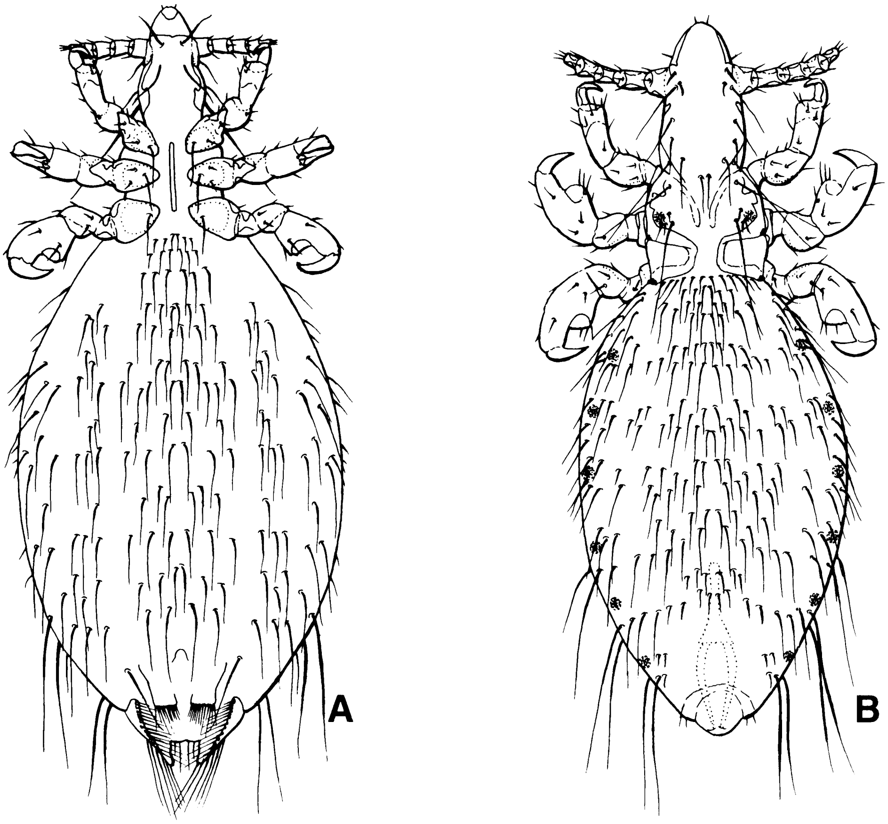


Figure 142. *Linognathus stenopsis* (goat sucking louse): ***A***, Ventral view of female; ***B***, dorsal view of male. Redrawn with minor modification by Jan Read from Ferris (1951); courtesy of Pacific Coast Entomological Society.

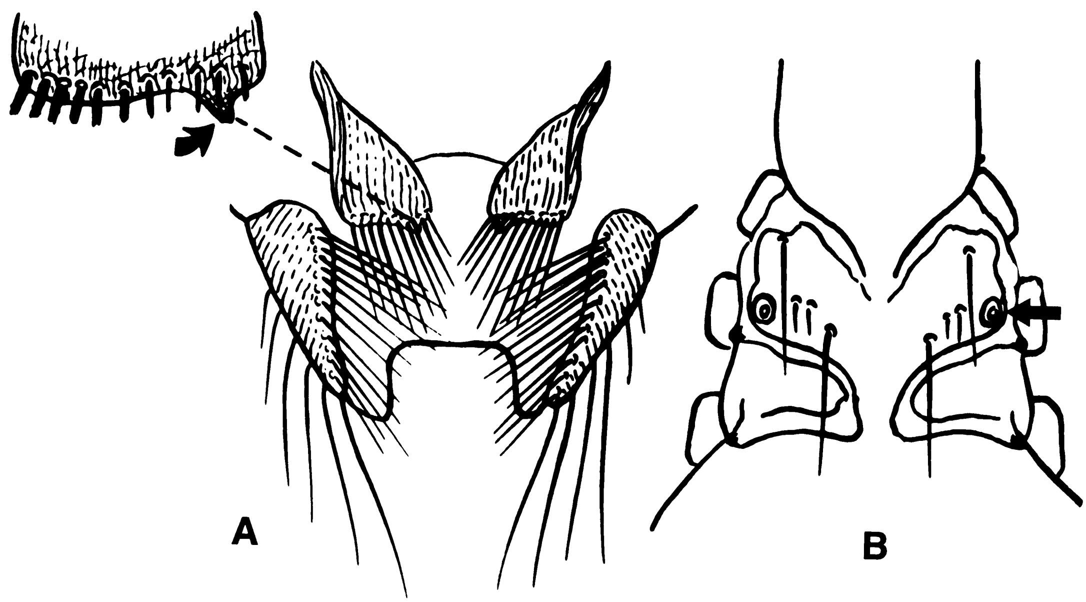


Figure 143. *Linognathus stenopsis*: ***A***, Small but distinct tooth (at arrow) on apex of female gonopod; ***B***, thoracic spiracle (at arrow) is not large and conspicuous. From Stojanovich and Pratt (1965), Key to Anoplura of North America, U.S. Department of Health, Education, and Welfare.

Severe infestations of the goat sucking louse seem to be rare, but when they do occur, they are more injurious than those of biting lice because of their bloodsucking habit (Roberts 1952). Two infestations of sheep in Nigeria were described by van Veen and Mohammed (1975): the sheep were burdened by gastrointestinal parasites and malnutrition but also suffered from large numbers of *L. stenopsis*, which produced a dry crustaceous seborrheic dermatitis and moderate anemia. Pratap et al. (1991) observed that 68% of a herd of Black Bengal goats in India were infested with *L. stenopsis*; the lice were collected mostly from the long-haired parts of the hind legs and back.

Linognathus vituli (longnosed cattle louse)

The common name for *Linognathus vituli*, the longnosed cattle louse, is derived from the shape of its head, which is long and narrow and about twice as long as broad (fig. 144). The antennae are not as long as the head (fig. 145). In front of the antennae, the head is long and pointed while the lateral margins of the head behind the antennae are near parallel. The first pair of legs is distinctly smaller than the second and third pair. The thoracic sternal plate is entirely lacking. The female gonopod has a well-developed sclerotized hook on the posterior margin (fig. 145), and male genitalia have parameres that are long and slender. The female averages 2.38 mm long and the male 1.8 mm (Kim et al. 1986).

An apparent phoretic relationship between *L. vituli* and a fly *(Musca lasiophthalma)* was recorded by Bedford (1929), who collected a nymph from the fly at Capetown, South Africa.

The longnosed cattle louse has accompanied domestic cattle, *Bos taurus*, to all parts of the world. Apparently it is more abundant in temperate and cold climates than in tropical areas. It is usually the most abundant louse of cattle in eastern Canada (Haufe 1962). In Korea, S.K. Kim (1968) found that about 15% of cattle were infested with *L. vituli*.

Life history. The following tabulation is taken from a report by Lancaster (1957), who determined the life cycle of *Linognathus vituli* in Arkansas:

	Number of days for development	
Period	**February**	**March**
Incubation	7–9	8–10
First-instar nymph	9	6–7
Second-instar nymph	4	3–5
Third-instar nymph	3	5
Preoviposition	2	2
Complete life cycle	25–27	24–29
Mean air temperature	5 °C	11.2 °C
Host skin temperature	35.5 °C	35.9 °C

The data in the tabulation agree quite well with those of Lamson (1918), who reported 23–27 days for a life cycle in Connecticut, and with those of Matthysse (1946), who reported 23–30 days and an average 25 days in New York State. Matthysse stated that the average oviposition rate is one egg per day.

Host-parasite relationships and economic importance. Cattle are both the type and usual host for *Linognathus vituli*. Roberts (1952) added that the longnosed cattle louse definitely prefers the dairy breeds of cattle as hosts and that it is more likely to infest young animals. Other collection records for this louse—such as reports by Ferris (1951) of its occurrence on wild boar *(Sus scrofa)* in Europe, on sheep, and on the domestic dog—can be attributed to collections of stragglers or from a temporary host. Becklund (1957) found it on goats in southern Georgia (United States) and Rao et al. (1977) on sheep in India, but these animals had been pastured with cattle and there was no evidence that the lice came from established infestations. However, Ahmed et al. (1977) found that sheep at Mandya, India, were heavily infested with *L. vituli* (and *Bovicola ovis*).

On cattle, the heaviest infestations are frequently found on the top and sides of the neck, the withers, and the dewlap (Lamson 1918, Matthysse 1946), but smaller numbers may be seen on the sides of the body, topline, belly, udder, rump, and perineum. Lewis et al. (1967) noted that when they were rearing lice on cattle, the longnosed cattle louse occupied the lower half of the body and the cattle biting louse (*Bovicola bovis*) occupied the upper half. If this is true in nature, it suggests some degree of antagonism between the two louse species. The longnosed cattle louse moves about less on its host than does the cattle biting louse; dense patches of *L. vituli* and their eggs can often be found on cattle.

It is difficult to assess the damage caused in the United States by *Linognathus vituli*, but in certain states it is found more frequently in herds of cattle than any other species of cattle louse. It often occurs in very high

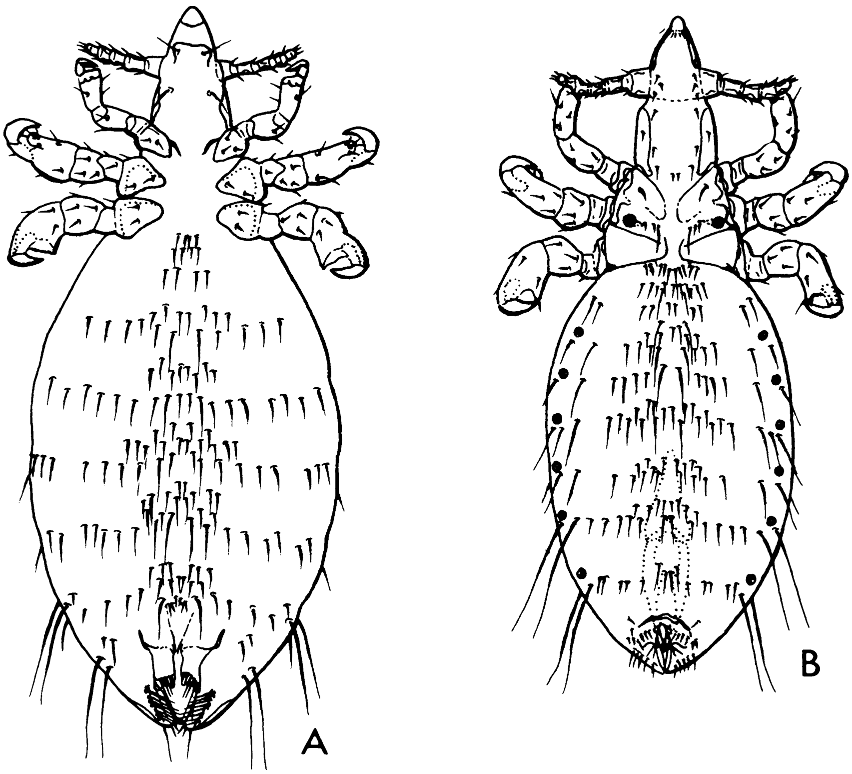


Figure 144. *Linognathus vituli* (longnosed cattle louse): ***A***, Ventral view of female; ***B***, dorsal view of male. Redrawn with minor modification by Jan Read from Ferris (1951); courtesy of Pacific Coast Entomological Society.

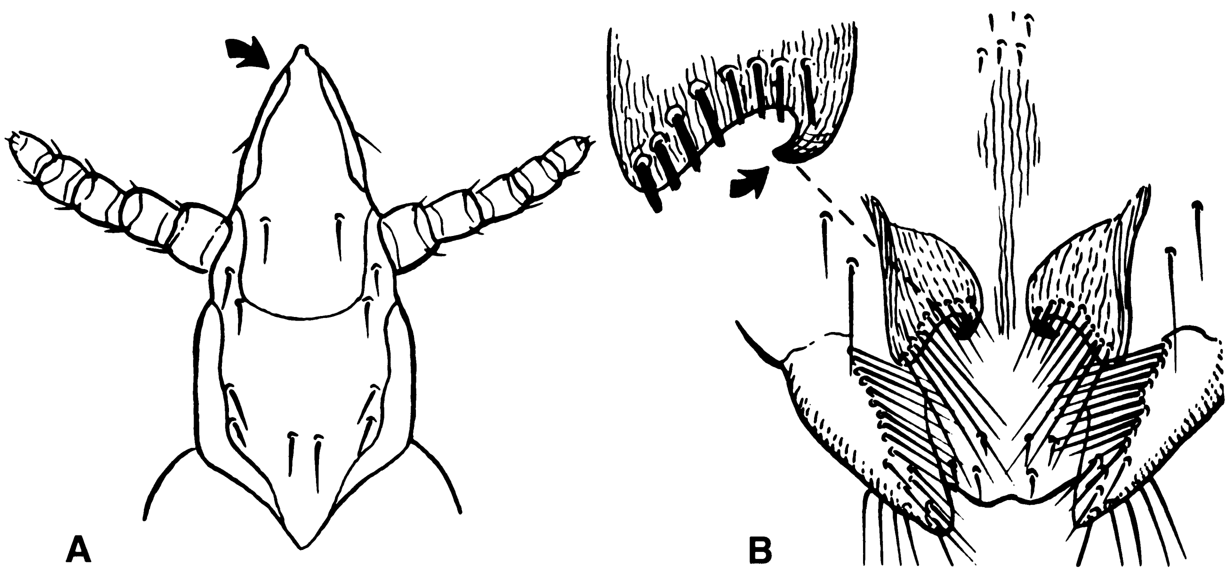


Figure 145. *Linognathus vituli*: ***A***, Head long and narrow (at arrow), and antennae shorter than head; ***B***, distinct hook (at arrow) on apex of female gonopod. From Stojanovich and Pratt (1965), Key to Anoplura of North America, U.S. Department of Health, Education, and Welfare.

numbers. Lancaster (1957) stated that the longnosed cattle louse was the most important species of cattle louse in Arkansas in 1952–53, at least in part because of its high populations. He found it in 23 of 55 herds examined, and as many as 343 lice/inch^2. Chalmers and Charleston (1980) noted that it was the most abundant sucking louse of cattle in New Zealand. Calves, yearlings, and undernourished cattle suffer more than do grown cattle in good condition. Burns et al. (1992) could not detect a significant loss in weight gain by naturally (perhaps lightly?) infested Ayrshire bull calves—three infested and three not. Nevertheless, heavily infested cattle on feed do not eat well, they do not gain weight properly, and their vitality is greatly lowered. Their unthrifty condition is indicated by their depressed behavior and the mangy appearance of their hair coat.

Lousy cattle spend a great deal of time scratching and rubbing against any convenient object, resulting in lost patches of hair; then these bare spots are sometimes rubbed until open, raw sores appear.

Other species of *Linognathus*

The genus *Linognathus* needs revision, but it will be a difficult undertaking because many bovid hosts are endangered species whose sucking lice are known only from the type specimens that were used to describe them. In appendix B, we list 40 of the 51 species that the genus was said to include (Kim and Ludwig 1978b), but it is not certain that all are valid. More than half of the 40 species are parasites of antelopes and other wild game animals in the family Bovidae in Asia and Africa.

Fourie et al. (1991) collected 3,881 specimens of *Linognathus oryx* from 22 gemsbok (*Oryx gazella*) in a herd of 24 in Orange Free State, South Africa. Young gemsbok were infested with a significantly larger number of lice than were older animals.

Horak et al. (1992a) collected *Linognathus antidorcitis, L. armatus, L. bedfordi*, and *L. euchore* from springbok (*Antidorcas marsupialis*), *L. oryx* from gemsbok (*Oryx gazella*), and *L. taurotragus* from kudu (*Tragelaphus strepsiceros*) in national parks in Namibia. The latter louse was also recovered from kudus at four locations in South Africa; it was more abundant than the chewing louse, *Bovicola* sp., or another sucking louse, *Haematopinus taurotragi* (Horak et al. 1992b).

The family Canidae are hosts for *Linognathus setosus* (already discussed) and two other sucking lice, both of which are rare, from wild Canidae. These rare Anoplura are *Linognathus taeniotrichus* from a South American fox, *Procyon (=Dusicyon) cancrivorous*, and *Linognathus fenneci* from the desert fox [*Vulpes (Fennecus) zerda*] of North Africa.

Linognathus vulpis was reported to be a parasite of *Vulpes reuppellii bengalensis* in Pakistan by Werneck (1952), but its present status is uncertain. Durden et al. (1990) did not find *L. vulpis* in Pakistan, but considered it a valid species because of records of its collection from *Vulpes vulpes* in Iran by Kim and Emerson (1971).

Kim and Weisser (1974) returned *panamensis* to *Linognathus* from *Solenopotes*, with the remark that it is close to *Linognathus breviceps* and to *Linognathus limnotragi. L. panamensis*, which appears to be a valid species, was described by Ewing (1927) from specimens collected from a dead Panamanian deer at the National Zoological Park in Washington, DC. It now appears probable that the louse had transferred to the deer from a South African Bovidae that was also at the park. Horak et al. (1989) collected 358 specimens of *L. panamensis* from 10 bushbucks (*Tragelaphus scriptus*) in South Africa.

Genus *Solenopotes*

Kim and Weisser (1974) revised *Solenopotes*. They recognized eight species: two from ungulates in the family Bovidae and six from deer (Cervidae). The two species from Bovidae appear to be aberrant forms whereas the other six seem to form a definite taxonomic group. The 6 are parasites of 6 genera of Cervidae, but they have not been found on 11 other genera. Kim and Weisser distinguished *Solenopotes* from *Linognathus* in that *Solenopotes* has a large, wide sternal plate and a continuous mesothoracic phragma. The abdominal dorsum of *Solenopotes* has a single transverse row of setae of various sizes. The male genitalia have a reduced subgenital plate and lyriform gonopods (see fig. 149). The females have prominent gonopods but usually lack the median genital plate. Females average 1.68 mm long and males 1.12 mm (Kim et al. 1986).

The genus *Solenopotes* is cosmopolitan, but species from wild animals (not in a zoological park) are restricted in distribution to that of their hosts.

Solenopotes capillatus

Enderlein (1904) described *S. capillatus* from a male collected from a cow in Germany, and not until 1921 did Bishopp describe the female in his first report of the species from North America. The little blue cattle louse (fig. 146), as *S. capillatus* is sometimes called, has a short, broad head and distinct, broad sensoria on antennal segments 4 and 5 (fig. 147). The large thoracic sternal plate has a concave anterior margin and a convex posterior margin. Abdominal segments 3–8 each have strongly protuberant spiracles (fig. 148) on pronounced sclerotized tubercules. Male and female genitalia are as shown in figures 149 and 150.

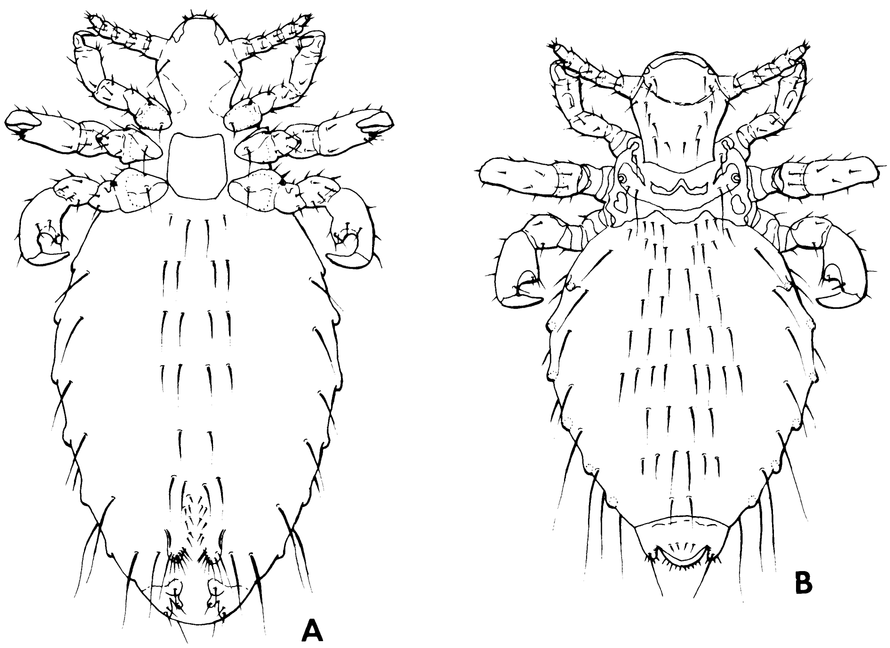


Figure 146. *Solenopotes capillatus*: ***A***, Ventral view of female; ***B***, dorsal view of male. Redrawn with minor modification by Jan Read from Ferris (1951); courtesy of Pacific Coast Entomological Society.

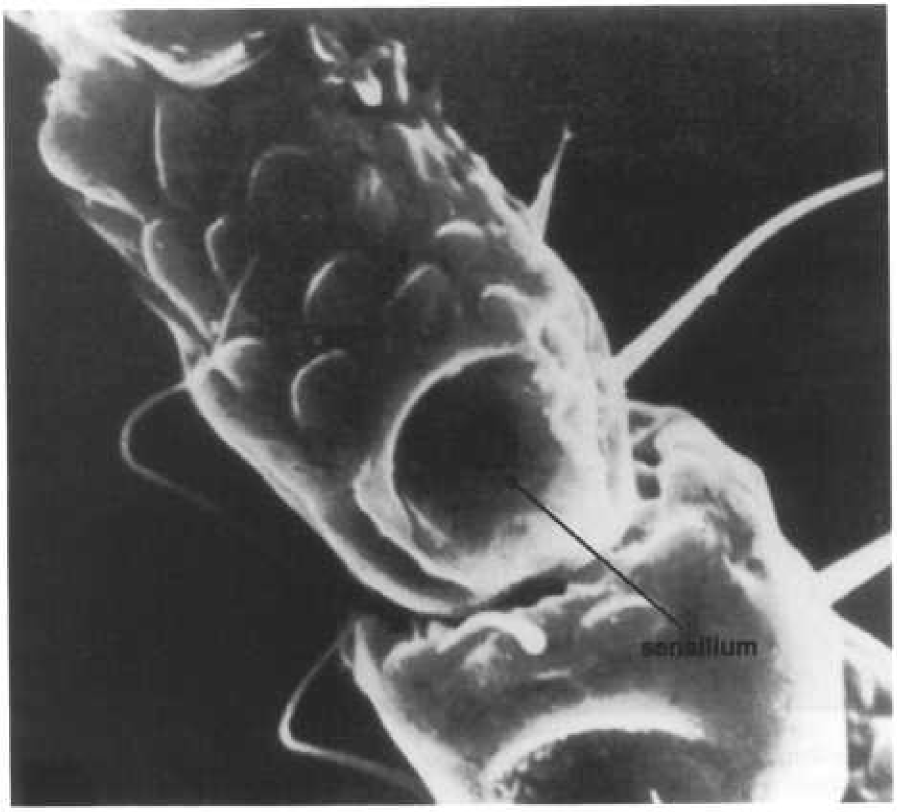


Figure 147. *Solenopotes capillatus*: Large sensillum in center is on antennal segment 5. SEM × 1,000. From Miller (1970), reprinted by permission of Journal of New York Entomological Society.

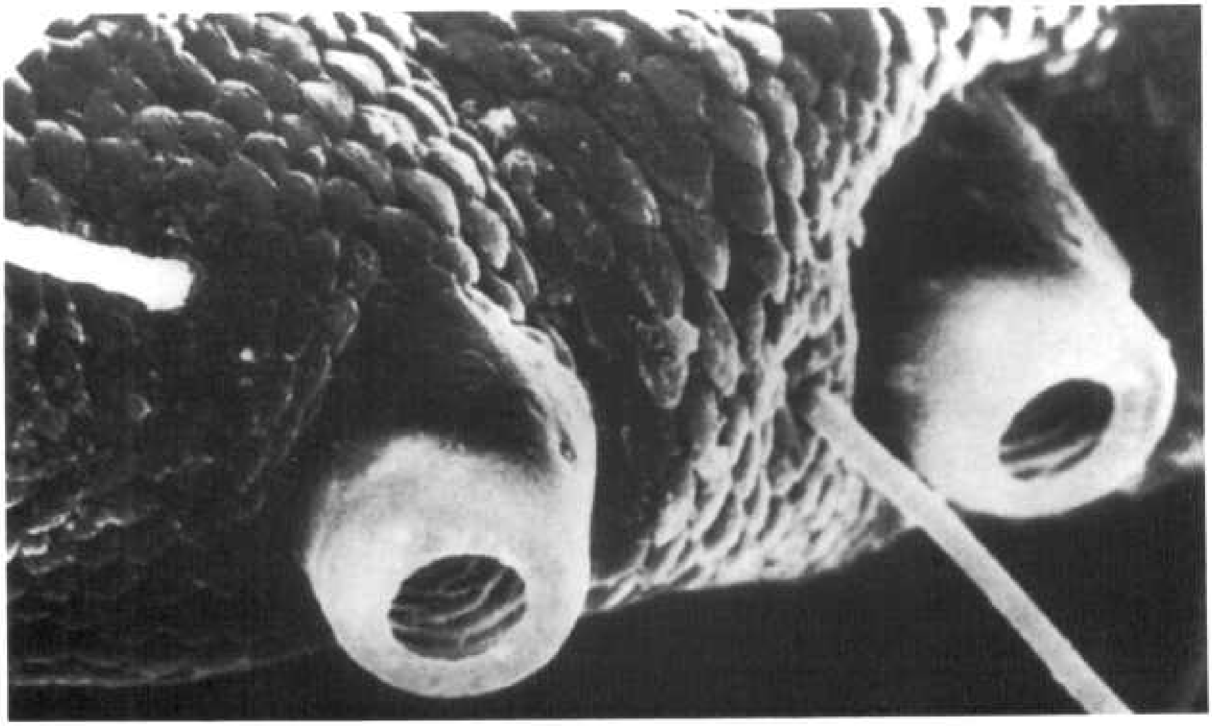


Figure 148. *Solenopotes capillatus*: Abdominal spiracles. SEM X 700. From Miller (1970), reprinted by permission of Journal of New York Entomological Society.

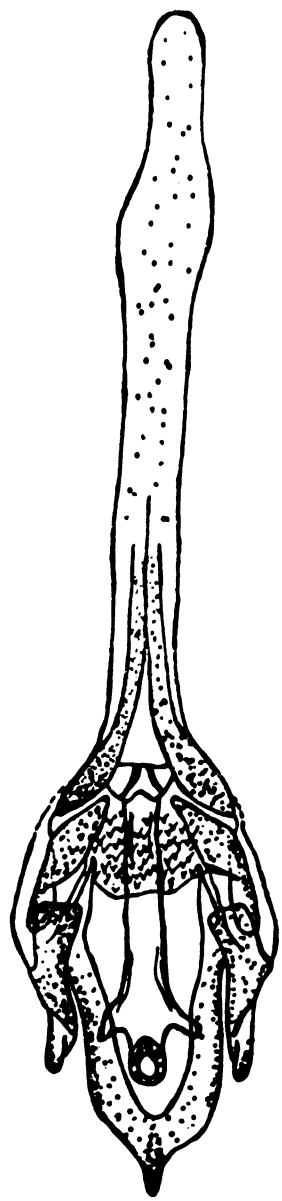


Figure 149. *Solenopotes capillatus*: Male genitalia. From Kim and Weisser (1974), reprinted by permission of Cambridge University Press.

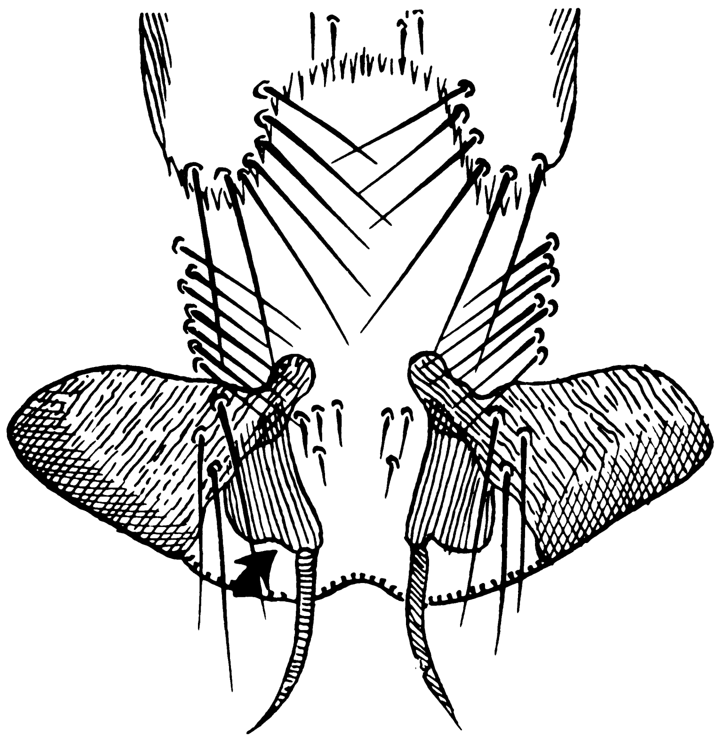


Figure 150. *Solenopotes capillatus*: Female terminalia. Note strong constriction of gonopod 8 at arrow. From Stojanovich and Pratt (1965), Key to Anoplura of North America, U.S. Department of Health, Education, and Welfare.

Apparently, early workers often confused *S. capillatus* with *Linognathus vituli* and other sucking lice of cattle, and *S. capillatus* was already well established in the United States when Bishopp (1921) published his first report. A similar situation occurred in South Africa, where *S. capillatus* was first reported by du Toit (1968) after it was widely distributed in that country.

Although its distribution may be discontinuous, *S. capillatus* is cosmopolitan on domestic cattle. In many parts of the eastern and southeastern United States, it is the most abundant species of cattle sucking louse. Also, DeFoliart (1957) found it to be the most abundant cattle louse in southeastern Wyoming, occurring in 31 of his 39 tests. S.K. Kim (1968) reported it to be the most common sucking louse of cattle in Korea, with 29% of examined cattle found to be infested.

Life history. The egg (fig. 151) of *Solenopotes capillatus* resembles that of *Linognathus vituli* but is somewhat smaller. Matthysse (1946) noted that the hair to which the egg is attached is often bent at the point of attachment; this has not been reported for other species of cattle lice. Females lay 2–3 eggs/day, and the eggs hatch 9–13 days later. Jensen and Roberts (1966) noted that oviposition ceases when the host's skin temperature drops to about 21 °C or lower. Each of the three nymphal stages requires 35 days for its growth. The preoviposition period is also 3–5 days. A complete life cycle from egg to egg requires 21 or 22 days (Kim et al. 1986).

Host-parasite relationships and economic importance. Domestic cattle (*Bos taurus*) are the type and normal host for *Solenopotes capillatus*. In addition, Mitchell (1979) reported collecting it from axis deer (*Axis axis*) in Nepal.

S. capillatus is frequently found on the neck, head, upper and front parts of the shoulders, and dewlap (Jensen and Roberts 1966). Those skin areas had intermediate skin temperatures—that is, between the higher temperatures found on the back and top of the shoulders when the cow is in the sun and the lower temperatures found on the cow's belly.

In the geographic regions where *S. capillatus* is the most abundant species of cattle louse, it is also the most damaging (Lancaster 1957). It apparently moves less than other lice, and dense patches of adults, nymphs, and eggs can be seen on the head, neck, and dewlap of heavily infested cattle.

Other species of *Solenopotes*

Six of the other seven species recognized by Kim and Weisser (1974) are parasites of Cervidae (see appendix B). Weisser and Kim (1973) redescribed *Solenopotes tarandi* from specimens collected from caribou in Alaska, because Mjöberg's (1915) type specimens from Swedish reindeer had been lost.

Solenopotes natalensis, a parasite of an African antelope (the steenbok), has been studied from less than a dozen specimens. It and *S. capillatus* are the two species that parasitize bovids; all others are from deer.

FAMILY MICROTHORACIIDAE

The family Microthoraciidae was established by Kim and Ludwig (1978b) to accommodate the genus *Microthoracius*, which was described by Fahrenholz (1916). Most specialists believe the genus is intermediate between Haematopinidae and Linognathidae. The family and genus contain four species, and all are parasitic on camels and their relatives, the mammalian family Camelidae.

Microthoracius have clearly evident eyes and a greatly elongated head. Some species have a head almost as long as an abdomen that is attached to the thorax dorsally. The thorax is small and short and has a distinct notal pit and sternal apophyseal pits and a poorly developed stigmal plate. All legs are similar in size and shape. The abdomen is densely covered with small, fine setae (fig. 152) but is without paratergites (Kim and Ludwig 1978b). Male genitalia are illustrated in figure 153.

The genus *Microthoracius* contains four species (see appendix B). One is *M. cameli*, a parasite of the Old World one-humped camel (*Camelus dromedarius)* (Ferris 1951). The other three parasitize llamas in South America, which also belong to the family Camelidae.

The three species found on llamas are *Microthoracius praelongiceps, M. minor*, and *M. mazzai*. It appears that any of the lice of llamas will transfer from any of the four llama species to another llama if they are in close contact with each other (Dale and Venero 1977). This may be a modern development that occurs only in nature conservatories where different species of llamas are kept together. However, there is also a question about the validity of the llama species. Windsor et al. (1992b) observed that since all are able to interbreed and produce fertile progeny, there may be only one species of llama.

Windsor et al. (1992a) found that untreated alpacas (*Lama pacos)* in Peru were universally infested with *M. praelongiceps*; the lice were a major cause of weight loss and lost wool production. The life history, host-parasite relationships, and economic importance of the

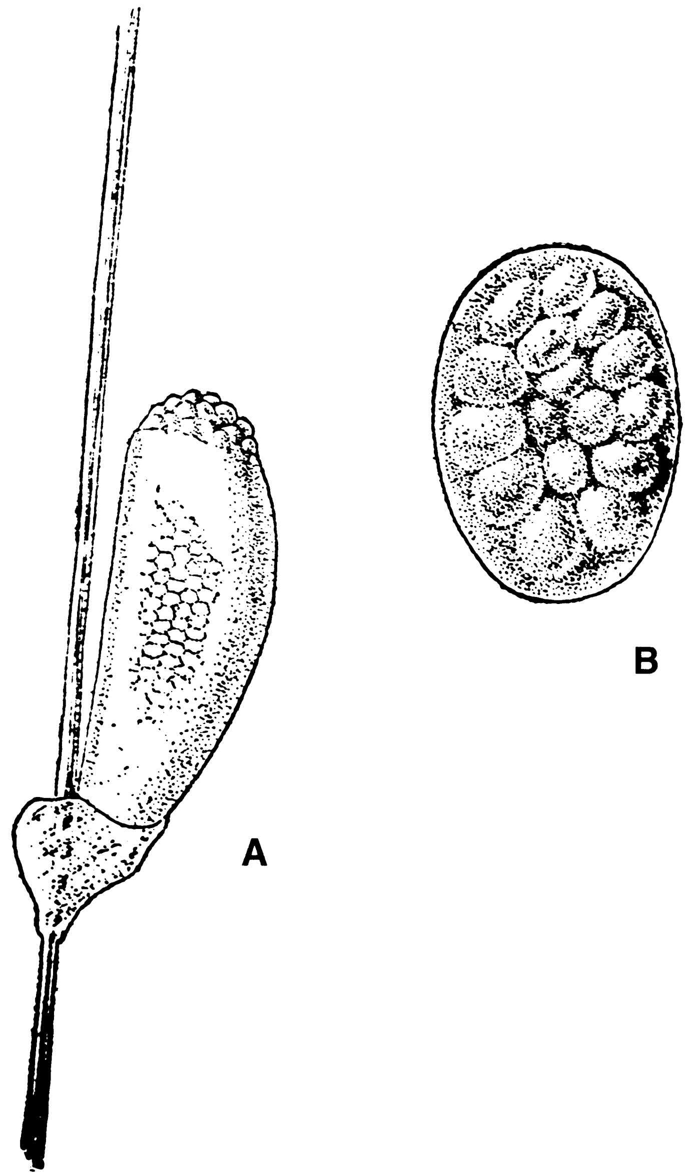


Figure 151. Egg of *Solenopotes capillatus*: ***A***, Attached to hair; ***B***, top view of operculum. From Bishopp (1921).

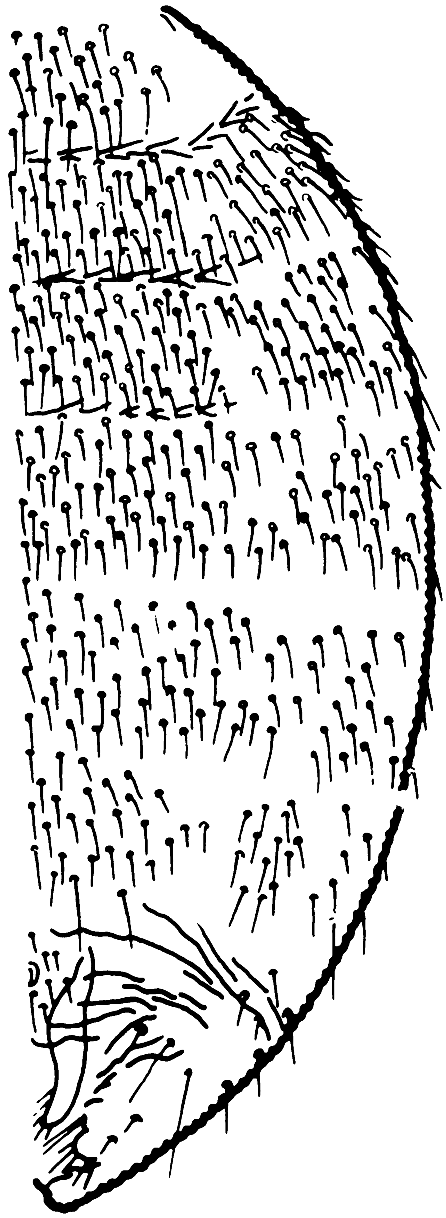


Figure 152. *Microthoracius cameli*: Ventral view of left half of abdomen, showing dense covering of small, fine setae. From Kim and Ludwig (1978a), reprinted by permission of Blackwell Science Ltd, Oxford, United Kingdom.

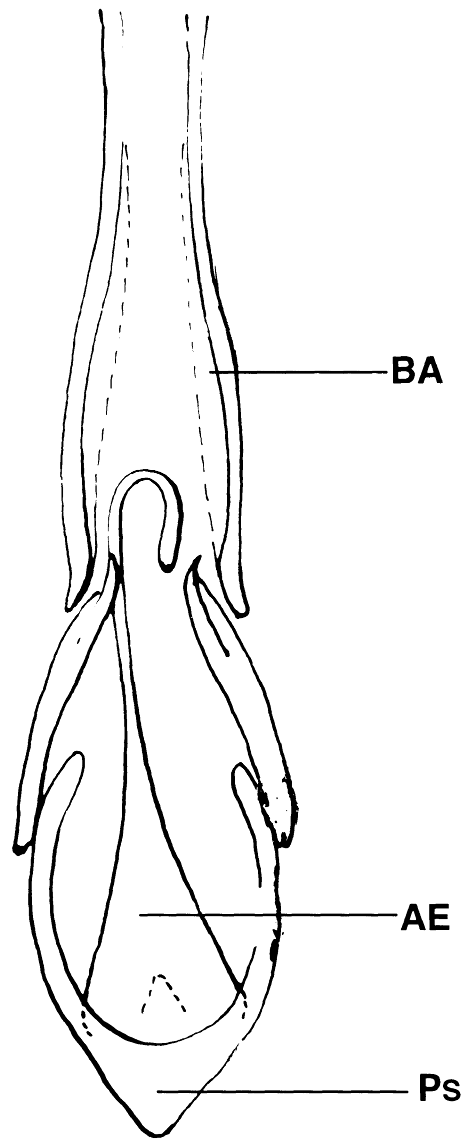


Figure 153. Male genitalia of *Microthoracius cameli*: **BA** = basal apodeme, **AE** = aedeagus, **Ps** = pseudopenis. From Kim and Ludwig (1978a), reprinted by permission of Blackwell Science Ltd, Oxford, United Kingdom.

sucking lice of the genus *Microthoracius* are largely unstudied.

FAMILY NEOLINOGNATHIDAE

Ewing (1929) may have been the first to recognize that the genus *Neolinognathus* is unique. He placed it in the subfamily Neolinognathinae, which Fahrenholz (1936) raised to family rank. Two species in the genus are parasites of elephant shrews (Macroscelidea: Macroscelididae) in the Ethiopian Zoogeographical Region. Kim and Ludwig (1978a) suggested that *Neolinognathus* transferred to elephant shrews at a point in geologic time after the genus broke off from the Polyplacidae.

The head of sucking lice in the family Neolinognathidae (fig. 154) is without external evidence of eyes, and the postantennal angle is not developed. The antennae are five-segmented. The thoracic sternal plate is divided into two longitudinal plates, and the thorax has a distinct notal pit. The forelegs are small and slender; the midlegs and hindlegs are subequal in size. The abdominal setae are minute. The abdominal spiracles are reduced to one pair, which are located on segment 8. Male and female genitalia are as shown in figure 154; the parameres are completely fused at their apex (Ferris 1951, Kim and Ludwig 1978a).

FAMILY PECAROECIDAE

The monotypic family Pecaroecidae was raised to family rank by Kéler (1963) and was recognized as such by Kim and Ludwig (1978b) and Kim et al. (1986). The peccary louse, *Pecaroecus javalii*, differs greatly from its closest relatives by being a very large louse (females average 6.9 mm long and males 6.3 mm) with a head about 3.5 times as long as wide and with the hindhead about four times longer than the forehead (fig. 155). The basal segment of the antennae is much broader than the other segments. The thorax is relatively short and is heavily sclerotized. The thoracic sternal plate is very narrow and long, or sometimes appears indistinct or absent (fig. 156). The first pair of legs is modified by having a large tibial thumb. The abdomen is long and approximately elliptical. Abdominal spiracles are present on segments 3–8. The paratergites are small, rounded, and tuberculiform (fig. 157). Male and female genitalia are as shown in figure 155.

The peccary louse has been collected only in the southwestern United States, but it probably has the same distribution as its host, the collared peccary (*Tayassu tajacu*), which is from most of South America north into the United States. Meleney (1975) reviewed the distribution of the louse in the United States; in general, it equaled that of its host. Babcock and Ewing (1938) noted that the type host, a 1-mo-old collared peccary, was heavily infested with lice; we have no reason to think that *P. javalli* is rare or even scarce. We are not aware of any reports of the louse from the other species of peccary: the white-lipped peccary (*Tayassu peccari*) and the tagua or Chacoan peccary (*Catagonus wagneri*). The white-lipped peccary has a broad Neotropical distribution, whereas the Chacoan peccary is known from only the Gran Chaco region of Bolivia, Paraguay, and Argentina.

FAMILY PEDICINIDAE

Kéler (1963) elevated Enderlein's (1904) subfamily Pedicininae to family rank. The family contains only the genus *Pedicinus* with its 16 species, all of which parasitize Old World monkeys (Primates: Cercopithecidae) (Kim and Ludwig 1978a) (appendix B). The Pedicinindae have a head with distinct eyes but without a prominent postantennal angle (fig. 158). The thorax has well-developed phragmata, but the notal pit is obscure. The sternal plate, sternal apophyses, and apophyseal plate are all lacking. Abdominal segments 4 (or 5) to 6 each have a pair of triangular paratergites, which are free from the abdomen at their apex (figs. 158, 159). The dorsal and ventral setae are always very small and are arranged in segmental rows.

It is difficult to define the geographical distribution of *Pedicinus* because of the large number of primates in zoological parks and research laboratories. In general, distribution of the lice is the same as that of their hosts, the Cercopithecidae.

Cercopithecidae, according to Honacki et al. (1982), includes 11 genera and 76 species. These animals are found in Africa, the Near East, southern Asia, Indonesia, Japan, Taiwan, and the Philippines. Many of the monkeys, such as the rhesus (*Macaca mulatta*), are widely used in research laboratories throughout the world.

Sucking lice in the genus *Pedicinus* are apparently benign parasites that seldom injure their hosts. In part, tenacious grooming by the monkeys keeps the louse population quite low. Old World monkeys obtained from their natural habitat are only occasionally infested (Kim et al. 1973). However, Mader et al. (1989) reported a particularly stubborn case of infestation of rhesus monkeys by *Pedicinus eurygaster* in which 100% of 69 animals were infested. Durden et al. (1990) found that macaques (*Macaca* spp.) were hosts of *Pedicinus obtusus*.

Apparently the life history of the *Pedicinus* is unknown.

FAMILY PEDICULIDAE

Leach (1817) established Pediculidae to accommodate *Pediculus*, the genus in which Linnaeus (1758) had

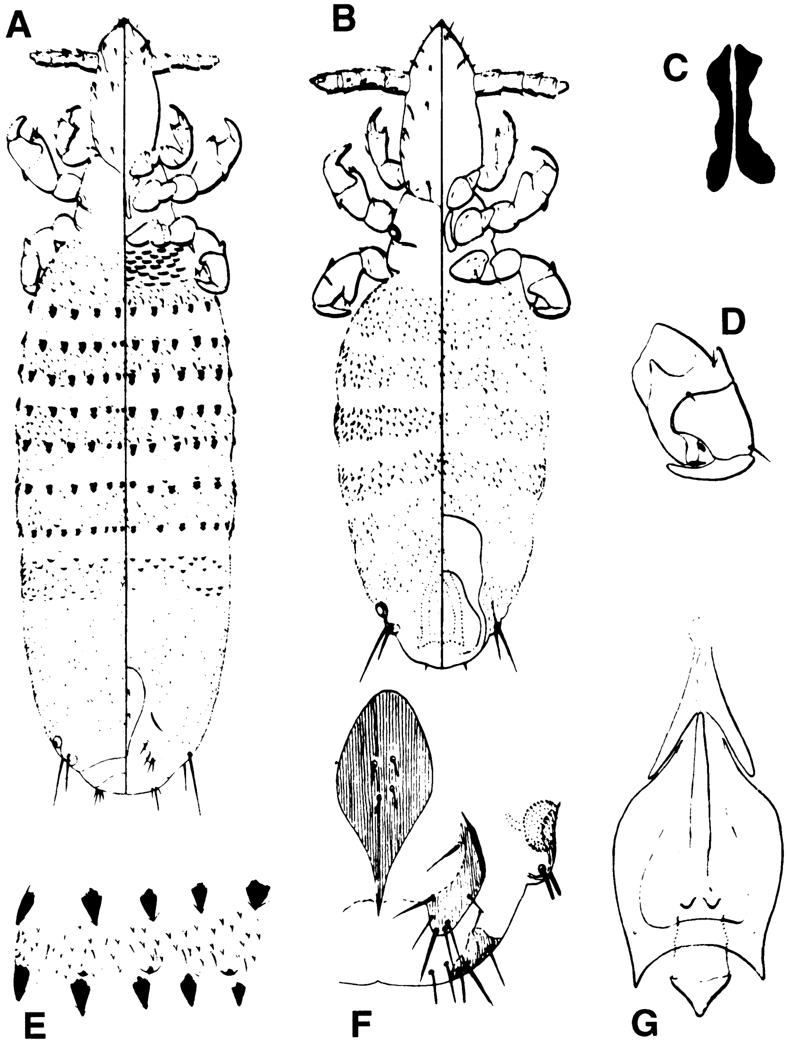


Figure 154. Taxonomic features of *Neolinognathus elephantuli*: ***A***, Dorsoventral view of female; ***B***, dorsoventral view of male; ***C***, thoracic sternal plate; ***D***, second and third tarsal claw; ***E***, abdominal ornamentation; ***F***, female terminalia, left half; ***G***, male genitalia. From Ferris (1951), reprinted by permission of Pacific Coast Entomological Society.

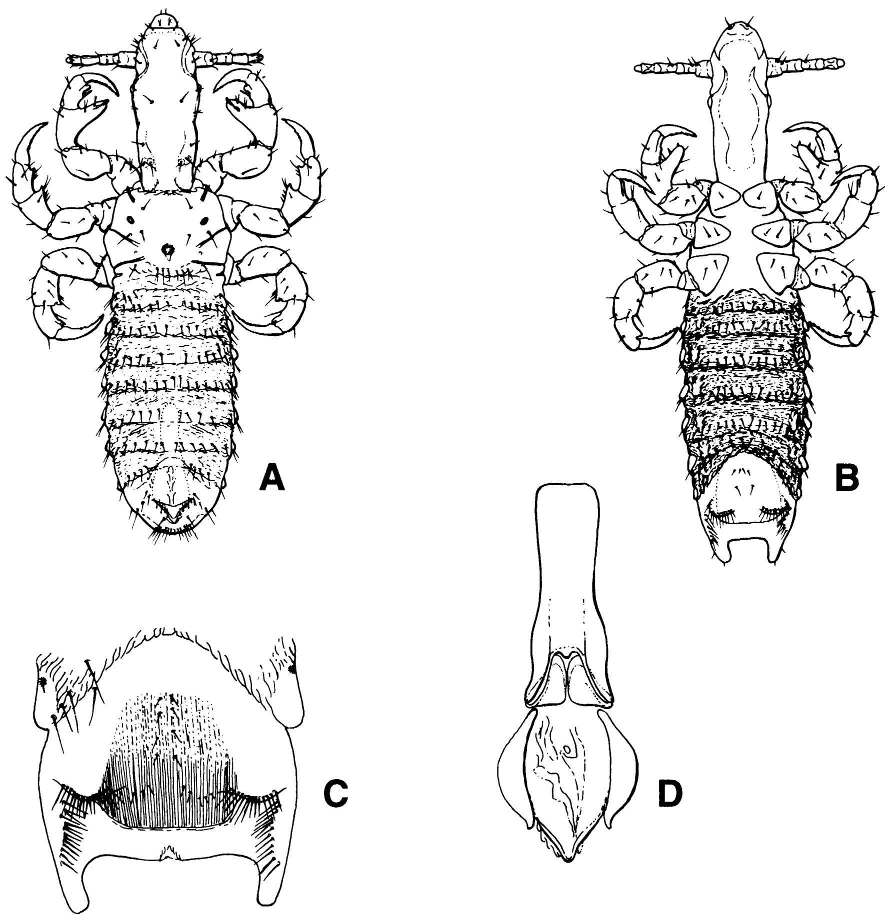


Figure 155. *Pecaroecus javalii*: ***A***, Dorsal view of male; ***B***, ventral view of female; ***C***, female terminalia; ***D***, male genitalia. Redrawn with minor modification by Jan Read from Ferris (1951); courtesy of Pacific Coast Entomological Society.

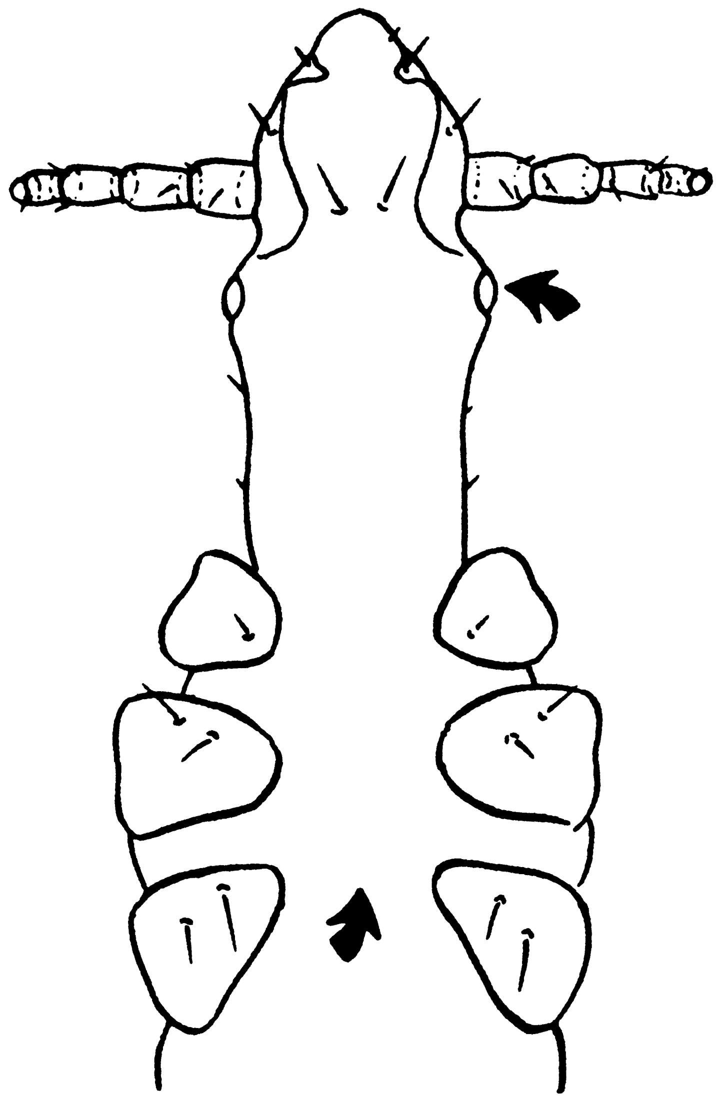


Figure 156. Outline of head and thorax of *Pecaroecus javalii*. Eyes are present (top arrow); sternal plate is indistinct or absent (bottom arrow). From Stojanovich and Pratt (1965), Key to Anoplura of North America, U.S. Department of Health, Education, and Welfare.

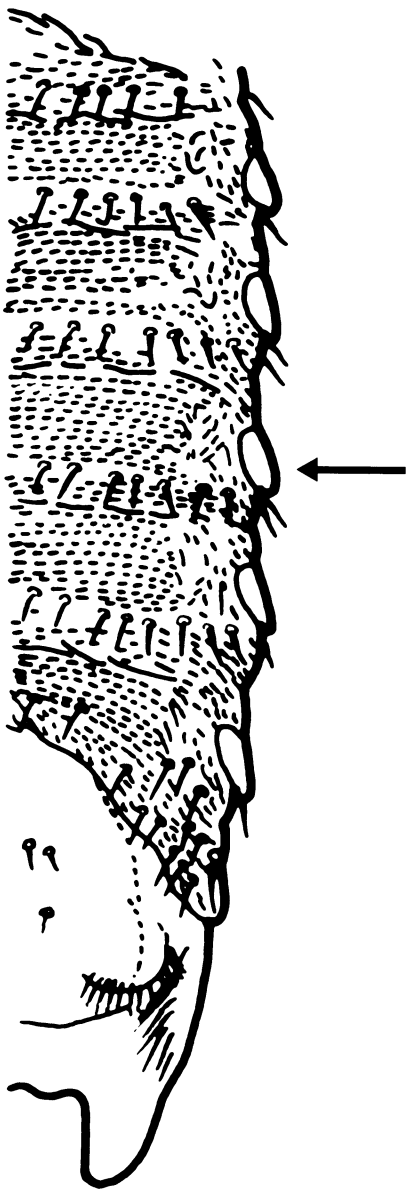


Figure 157. *Pecaroecus javalii*: Ventral view of left half of abdomen. Paratergites are small, rounded, tuberculiform; five are visible here. From Kim and Ludwig (1978a), reprinted by permission of Blackwell Science Ltd, Oxford, United Kingdom.

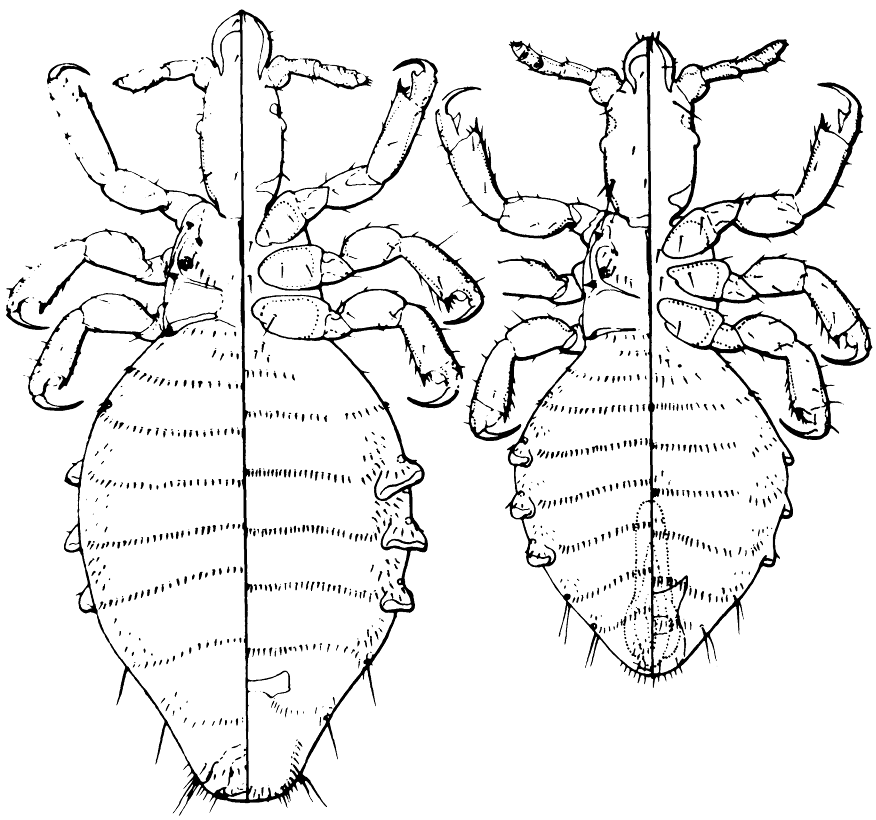


Figure 158. *Pedicinus obtusus*: Dorsoventral views of female (left) and male (right). From Ferris (1951), reprinted by permission of Pacific Coast Entomological Society.

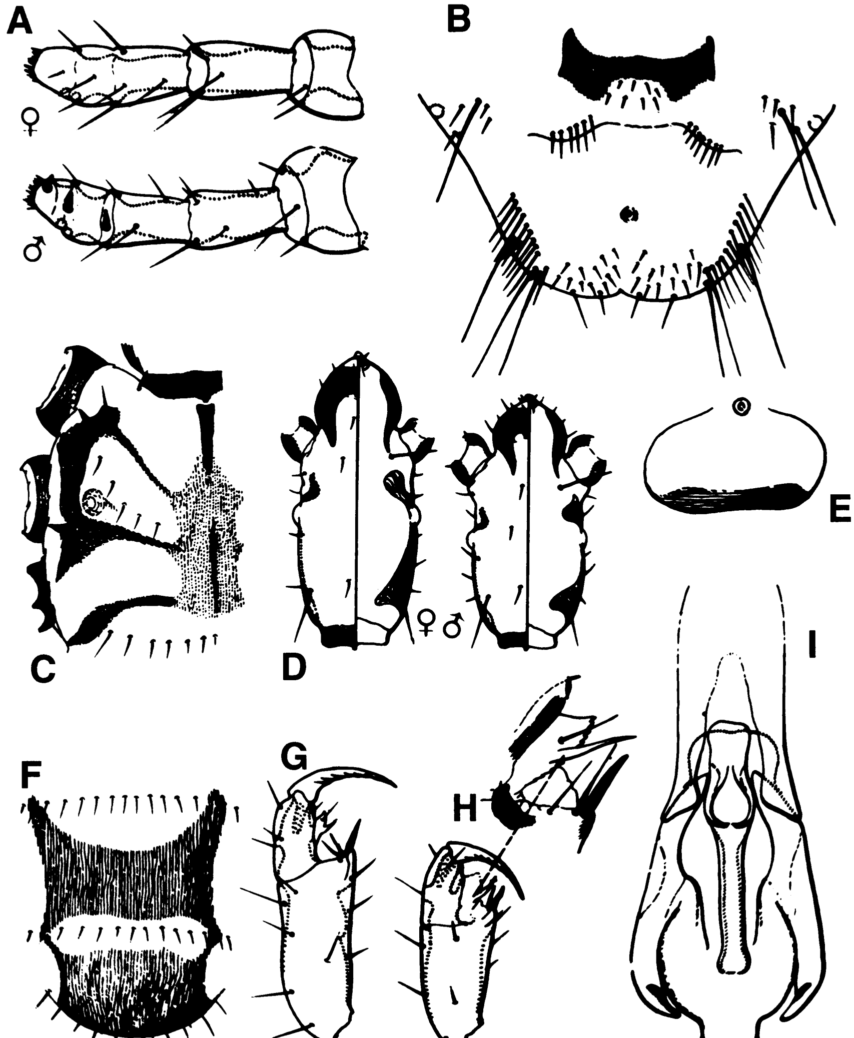


Figure 159. Taxonomic details of *Pedicinus obtusus*: ***A***, Antennae; ***B***, female terminalia; ***C***, thoracic notum; ***D***, head; ***E***, paratergites are found on abdominal segment 4(or 5)–6 and are marginally free; ***F***, male genital plate; ***G***, tarsal claw of prothoracic leg; ***H***, tarsal claw of meso- and metathoracic legs; ***I***, male genitalia. From Ferris (1951), reprinted by permission of Pacific Coast Entomological Society.

placed all chewing and sucking lice. Leach (1815) had earlier separated chewing and sucking lice into different genera, but placed all parasitic lice in his order Anoplura. As recently as 1891, Osborn referred to all sucking lice as Pediculidae, and it remained for later authors to divide the sucking lice into a number of families.

At present, Pediculidae contains only one genus: *Pediculus* (Kim and Ludwig 1978b). All other genera have been moved to other families. Certainly, as Kim and Emerson (1968) remarked, the task of presenting a systematic arrangement is not complete and the classification of the Pediculidae remains unsettled. In appendix B, we list one genus with three species.

The Pediculidae are distinguished by having a relatively short head that is constricted posteriorly into a short neck (fig. 160). They have well-developed eyes. The stylets and tubes that make up the mouthparts are shown in cross section in figure 161. The sternal plate is weakly developed or absent. All legs are about the same size; the tarsal claws are slender. The abdomen is long and membranous. Each lateral lobe is well developed and has a sclerotized paratergite that is attached (not free at its apex). Six pair of abdominal spiracles are completely enclosed by the paratergites. The abdominal setae are arranged in transverse fields, not in rows.

The best known species, *Pediculus humanus*, is a human parasite. It exists as two subspecies: the body louse (*P. h. humanus*), which attaches its eggs to clothing, and the head louse (*P. h. capitis*), which attaches its eggs to hairs on the head and other body parts. The collection of a body louse from mummified human remains in West Greenland was reported by Bresciani et al. (1983), who estimated that the corpse dated back to A.D. 1000–1350. They also collected several head lice from other corpses that dated back to A.D. 1450 (±50 yr).

Of the two subspecies, the body louse is more feared because it is the vector of epidemic typhus and epidemic relapsing fever—diseases that have in past times killed millions of people—whereas the head louse has never been associated with those diseases (Michigan State University 1990). The body louse may also have been a vector in limited outbreaks of murine typhus, a relatively mild febrile illness of humans (Azad 1990). According to Vaughan and Azad (1993), the body louse hemolyzes ingested erythrocytes rapidly and the blood meal remains liquified in the gut, a condition that favors acquisition of the causative organism of murine typhus by the louse.

Body lice are 10%–20% larger than head lice, tend to have more slender antennae, often are lighter colored, and have less-pronounced constrictions between the abdominal segments. Intermating between the two subspecies can occur, and it has been reported that head lice confined to the human body will, after four generations, acquire the morphological characteristics of body lice (Michigan State University 1990). The sequence of skin reaction to head lice infestation in a volunteer was reported by Mumcuoglu et al. (1991). The stages were (1) no clinical reaction, (2) a rash and medium itching, (3) a small, burning, localized reaction with intense itching, and (4) diminished rash and less itching. In their study of 2,643 school children in Israel, they found that 50 louse-infested children were more likely than uninfested children to have localized skin reactions, itching, skin peeling as a result of scratching a feeding site, and red, crusted eyelids.

Fan et al. (1992) decided that long-haired school girls in Taiwan were more susceptible to head lice than were boys; girls had 11–37 lice per person and a mean infestation of 10 lice per person. Of 2,160 lice collected, 83% were nymphs.

Mumcuoglu et al. (1990b) used a special lice comb with 12 teeth/cm to conduct surveys for head lice incidence. They combed the hair of the subject and removed nits (eggs, living and dead), nymphs, and adult lice. In a survey conducted in Israel, they found that children with brown or red hair had a higher incidence of head lice than those with black or blond hair, but they did not find a difference in incidence between boys and girls (Mumcuoglu et al. 1990b). The same team, Mumcuoglu et al. (1993), found that of 304 immigrants to Israel, 65% were infested with head lice and 39% with body lice.

Durden and Musser (1991) collected *P. humanus* from domestic dogs in Sulawesi, Indonesia; they considered the infestation an "accidental host-parasite association."

The other two species of *Pediculus* listed in appendix B are *Pediculus mjobergi*, a parasite of South American howler monkeys and spider monkeys (family Cebidae), and *Pediculus schaffia*, a parasite of a chimpanzee in the mammalian family Pongidae.

FAMILY POLYPLACIDAE

With its 20 genera and 190 species, Polyplacidae is the largest family of Anoplura (Durden and Musser 1994a). It was established as a subfamily of Haematopinidae by Fahrenholz (1912), moved to Hoplopleuridae by Ferris (1951), and elevated to family rank by Kéler (1963). The larger genera of Polyplacidae are *Polyplax*, *Fahrenholzia*, *Neohaematopinus*, and *Eulinognathus*, which are parasites of Rodentia and Insectivora. Durden (1991a) provided a world list of *Neohaematopinus* and

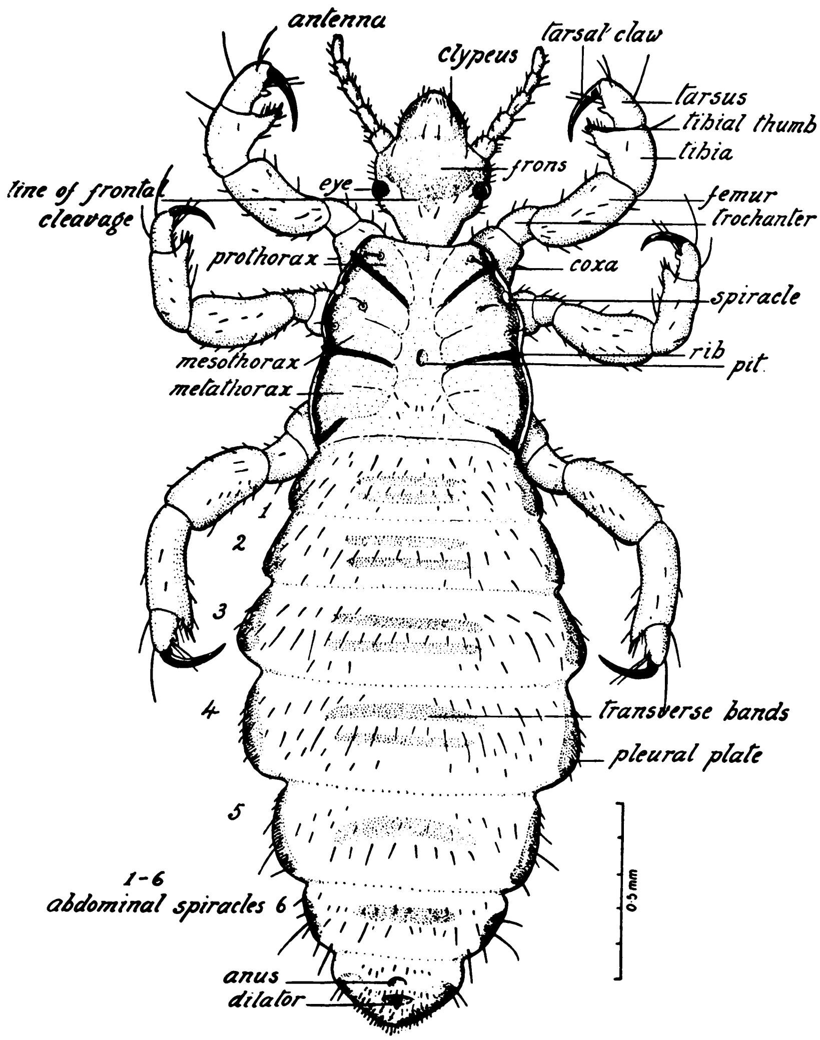


Figure 160. *Pediculus humanus* (body louse): Dorsal view of male, with principal parts labeled. From Keilin and Nuttall (1930), reprinted by permission of Cambridge University Press.

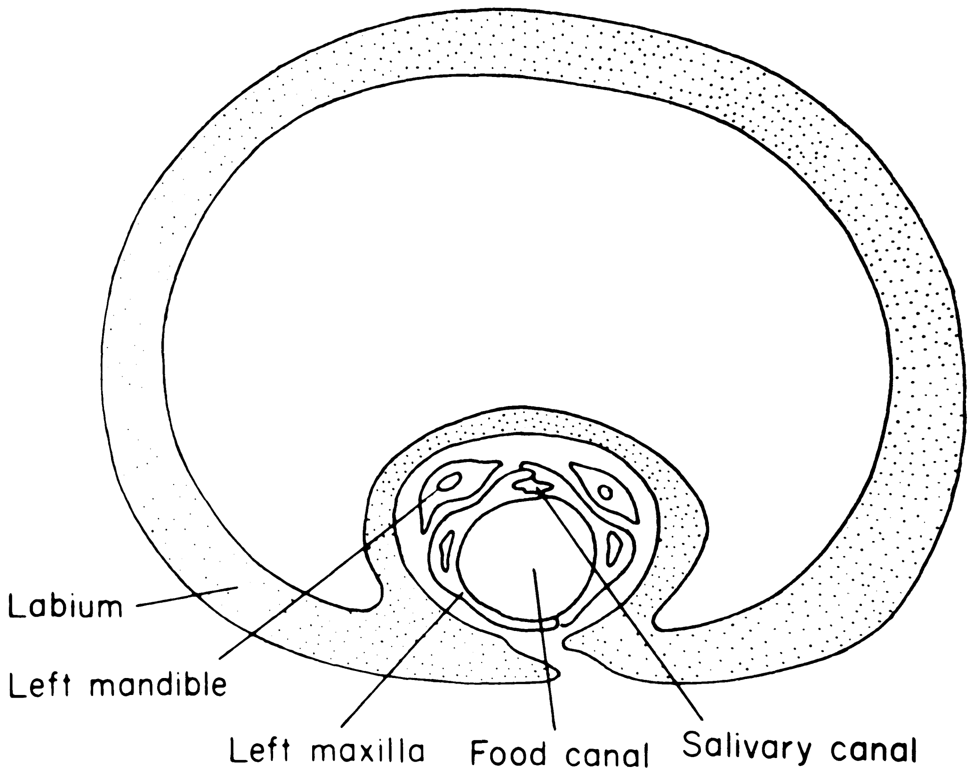


Figure 161. *Pediculus humanus*: Cross section of mouthparts. From Marshall (1981), reprinted by permission of Academic Press Ltd, London.

hosts for each of the 32 species; Kim and Ludwig had estimated that the genus contains 41 species. *Neohematopinus sciuri* was one of three core species of Anoplura occurring on the gray squirrel (*Sciurus carolinensis*) in Jacksonvile, Florida; 96 of 180 squirrels were infested (Wilson et al. 1991). *Lemurphthirus* has three known species, all of which are parasites of bushbabies (mammalian family Galagonidae), a group of lemurs found in Africa (Durden 1991b). Other genera parasitize rabbits and hares (order Lagomorpha) and prosimian Primates. Many genera are ill-defined and merely serve to group species temporarily. But as Johnson (1960) stated, we do not know enough about the full range of species to be able to divide genera at this time and must await the collection and description of species not now known before revision of Polyplacidae can be undertaken.

Polyplacidae are sucking lice with five-segmented antennae that are usually sexually dimorphic. There is no external evidence of eyes (Johnson 1960). The mesothoracic phragmata are usually evident, and the sternal plate is usually well developed (fig. 162) and only rarely absent. There is no notal pit. Forelegs are usually small and slender; midlegs and hindlegs are subequal in size and shape. Six abdominal spiracles are present. The sternal plate of abdominal segment 2 does not extend laterally to articulate with the corresponding paratergite. The abdomen is illustrated in figure 163 (Kim and Ludwig 1978b, Kim et al. 1986).

The species of Polyplacidae that interacts most often with humans is *Polyplax serrata*, commonly found on the house mouse (*Mus musculus*) worldwide and on laboratory white mice, and less often on wild mice such as the Old World or long-tailed field mouse (*Apodemus sylvaticus*) (Johnson 1960). Another species, *Polyplax spinulosa* (fig. 163), is primarily a parasite of Norway rats (*Rattus norvegicus*) and roof rats (*Rattus rattus*) (Linardi et al. 1994), but is also a pest of laboratory rats (Pratt and Karp 1953, Kim et al. 1973) and of the rice rat (*Orozomys palustris*) in Tennessee (Durden 1988). Hansens (1956) found *P. spinulosa* to be quite common in New Jersey; 1,692 of 2,759 Norway rats (61.3%) examined in a survey were infested. The survey covered a period of 17 mo; the average by month of lice per rat varied from 6.7 to 164.8. The most heavily infested rat had 16,044 lice. Volf (1991) described the rickettsia-like organisms, the symbionts, that develop in *P. spinulosa* and appear to be essential to the lice as producers of vitamins.

Murray (1961) demonstrated that self-grooming is the principal factor that regulates the distribution and abundance of *Polyplax serrata* on the house mouse (*Mus musculus*). Bell et al. (1962) found that a limb disability that prevented normal grooming by mice was the cause of heavy infestations of *Polyplax serrata* when mice were separated from other mice. Lodmell et al. (1970), in a continuation of the research by Bell et al., found that mutual grooming by normal mice maintained the louse burden at a low level in a stable association between several mice. However, if the association was disturbed by daily changes of the mice so that their living space was constantly occupied by strangers, then mutual grooming declined and louse populations increased dramatically.

Ratzlaff and Wikel (1990) used *P. serrata* to demonstrate an inducible anamnestic resistance in laboratory mice.

Roberts (1991a,b) found that *P. serrata* occurs quite commonly on the Polynesian water rat (*Rattus exulans*) on some of the smaller islands of New Zealand, but that the host has been displaced from the two large islands.

Both *Polyplax serrata* and *P. spinuosa* have a cosmopolitan distribution.

Although they are easy to control, both lice species sometimes establish themselves in laboratory colonies of white mice and rats and become so numerous that they injure or even kill their hosts (Oldham 1967).

In a study of host-parasite relationships between gerbils (*Gerbillus andersoni allenbyi*) and sucking lice in Israel, Lehmann (1992a) found that *Polyplax gerbilli* significantly reduced general host physical condition even though it did not cause anemia in the host. Numerous lice also had a negative effect on reproduction of the flea *Synosternus cleopatrae* (Siphonaptera: Pulicidae) when gerbils were infested with both ectoparasites (Lehmann 1992b). Durden and Musser (1992) described *Polyplax melasmothrixi*, a new species of *Polyplax* from a montane shrew rat in Sulawesi, Indonesia.

Two species of *Haemodipsus* are also of passing interest: *H. setoni* from the black-tailed jack rabbit (*Lepus californicus*) and *H. ventricosus* (fig. 164), a common parasite of domestic rabbits worldwide whose type host is the European rabbit *(Oryctolagus cuniculus*).

Thomas et al. (1990) collected two species of *Fahrenholzia* from different hosts in Texas, but they were uncertain if the lice were host specific or if the hosts merely inhabited separate niches at the same location.

FAMILY PTHIRIDAE

Ewing (1929) used the genus *Pthirus* as the type when he described the family Pthiridae. The genus had long been recognized as having several unique morphological characteristics (Leach 1815) which caused Ferris (1951) to place it in the subfamily Pthirinae of

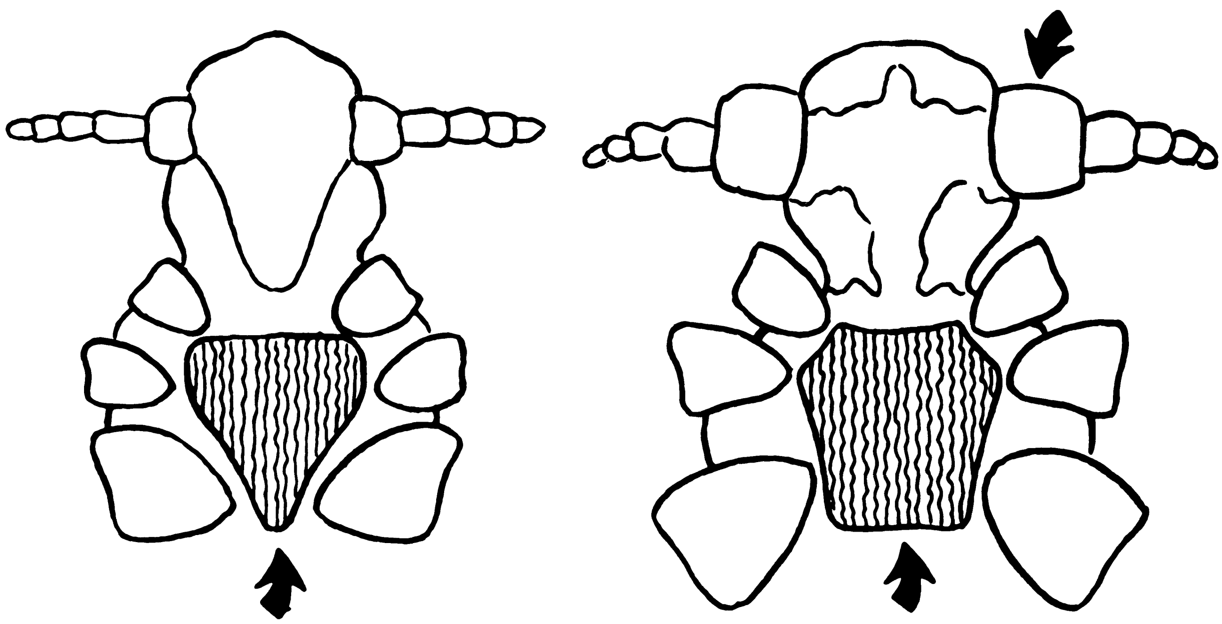


Figure 162. Shapes of the sternal plate (lower arrows) and the first antennal segments (upper arrow) are aids in identifying *Polyplax*. From Stojanovich and Pratt (1965), Key to Anoplura of North America, U.S. Department of Health, Education, and Welfare.

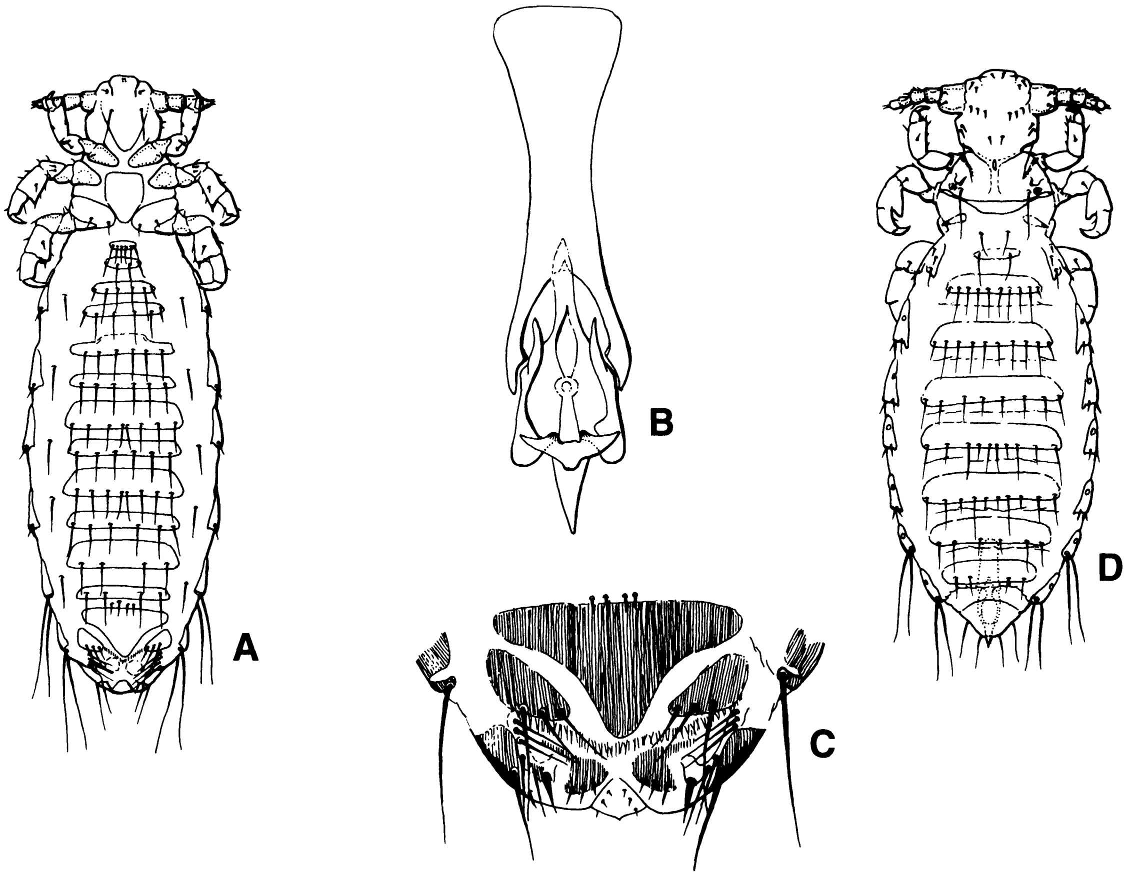


Figure 163. *Polyplax spinulosa*: ***A***, Ventral view of female; ***B***, male genitalia; ***C***, female terminalia; ***D***, dorsal view of male. Redrawn with minor modification by Jan Read from Ferris (1951); courtesy of Pacific Coast Entomological Society.

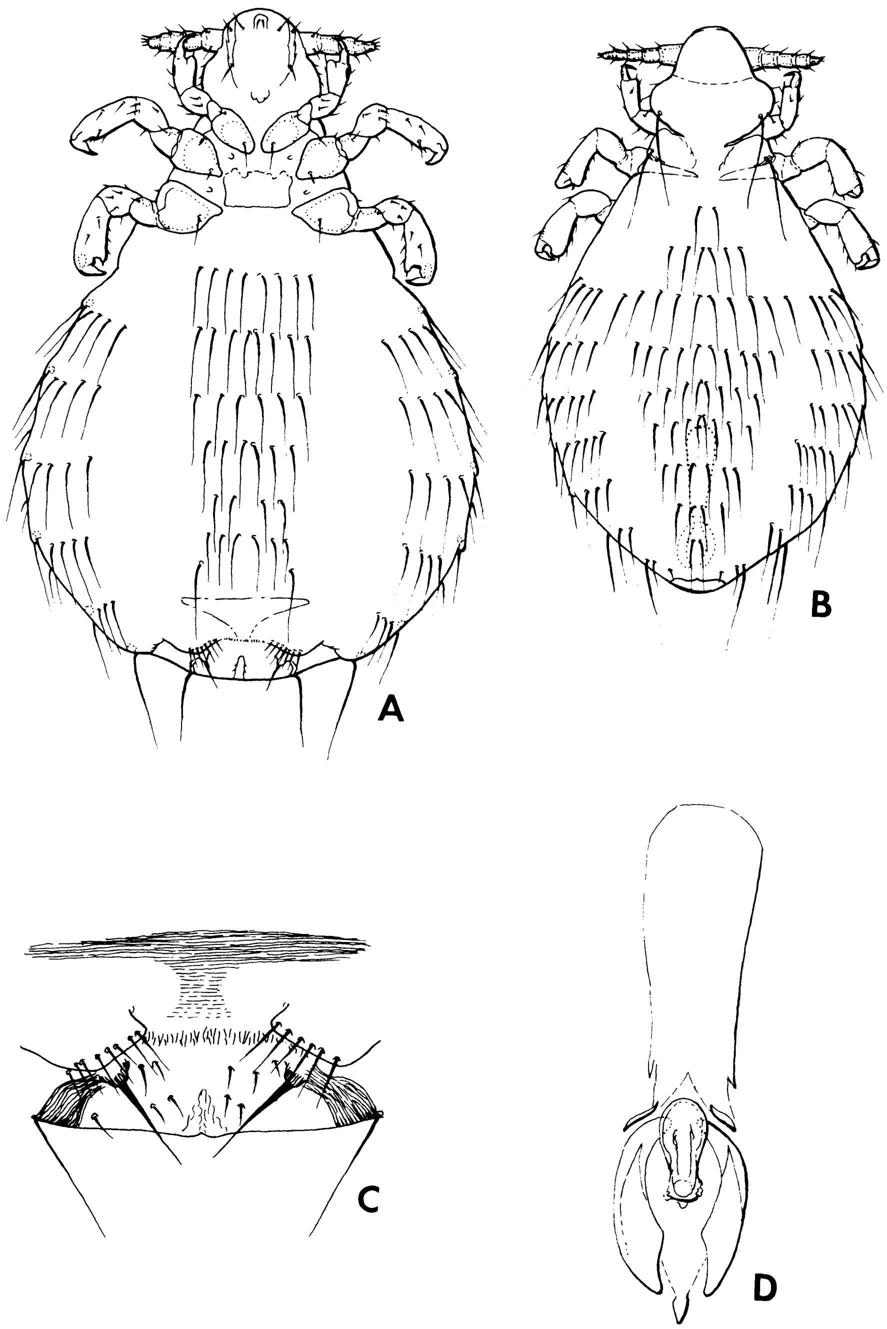


Figure 164. *Haemodipsus ventricosus*: ***A***, Ventral view of female; ***B***, dorsal view of male; ***C***, female terminalia; ***D***, male genitalia. Redrawn with minor modification by Jan Read from Ferris (1951); courtesy of Pacific Coast Entomological Society.

Pediculidae and ignore Ewing's earlier family rank for the group. Kim and Ludwig (1978b) accepted Pthiridae as a family and provided a key to the species and a description of the family. Kim and Emerson (1968) noted that three spellings of the generic name have been used (*Pthirus, Phthirus,* and *Phthirius*), but because Leach had used *Pthirus* in 1815, that spelling has priority.

Pthirus can be recognized by the short head; the head is also much narrower than the thorax and is never constricted into a neck (fig. 165). The forelegs are smaller and much more slender than the midlegs and hindlegs, which are large and have greatly enlarged claws. The abdomen is relatively small and about as long as its basal width. Segments 5–8 each have prominent, heavily sclerotized paratergal lobes, and each has several large setae. The last paratergite (fig. 165) is especially prolonged. Two species of *Pthirus* were recognized by Ferris (1951): *P. pubis,* the crab louse of humans, and *P. gorillae,* from the gorilla of Central Africa. *P. pubis* is a cosmopolitan parasite of humans that attaches itself to hairs, principally in the pubic and perianal areas, and less often infests the armpits, beard, and eyebrows (Clay 1973). Crab louse eggs are also attached to body hairs in the regions that the louse inhabits (fig. 166). Up to 100 pubic lice have been counted on the eyelashes of a single person (Hay 1990, Michigan State University 1990).

The incidence of crab lice in a group of young adults increased from 7/1,000 in 1977 to 14.9/1,000 in 1983 and then declined to 4.6/1,000 in 1987; incidence was highest in the cooler months (Gillis et al. 1990). In a survey of the prevalence of the crab louse among Nigerian prostitutes, Imandeh (1993) found that 53% were infested, with the highest rate occurring in women 40–49 yr old. Replogle et al. (1994) described a technique for identifying host DNA from crab louse excreta.

This louse has also been reported from dogs (Frye and Furman 1968), but Kim et al. (1986) said that such infestations are probably accidental and not self-sustaining.

Nuttall (1918) found that a complete life cycle requires 22–26 days.

From the time that Ewing (1927) described *Pthirus gorillae* from two first-instar nymphs, 40 yr elapsed without additional specimens being reported, and some workers questioned the validity of the species. However, Kim and Emerson (1968) obtained two females that had been collected from a young captive gorilla in the Congo, Africa, and described the adult stage.

FAMILY RATEMIIDAE

Ferris (1951) considered *Ratemia* to be one of 16 genera in the subfamily Polyplacinae of the family Hoplopleuridae. He stated that it was very difficult, because of host relationships, to not place *Ratemia* in either Haematopinidae or Linognathidae, but that its morphology caused it to be placed with the sucking lice of rodents, the Polyplacidae. Kim and Ludwig (1978b) resolved the problem by establishing the family Ratemiidae for the single genus and its two species.

Ratemia has been reported from only the Ethiopian Zoogeographical Region, where it occurs on two species of Equidae.

The Ratemiidae (fig. 167) have a head that is without external evidence of eyes and an antennal-ocular segment that is much wider than the clypeus. The mesothoracic and metathoracic phragmata are distinct, with the mesothoracic phragmata connected across the dorsum. The sternal plate is short and wide. The sternal apophysis and apophyseal pit are absent; the notal pit is present but small. The abdomen is without tergal and sternal plates except in the genital area. The abdominal setae are short and arranged in eight or more irregular rows. Three pair of paratergites are located on segments 4–6 and are free from the body wall at their posterior margin.

The two species of the genus and the family are *Ratemia squamulata,* from the domestic donkey (*Equus asinus*) and from Burchell's zebra (*Equus burchelli*) (Ferris 1951), and *Ratemia bassoni,* also from Burchell's zebra (Fiedler and Stampa 1958).

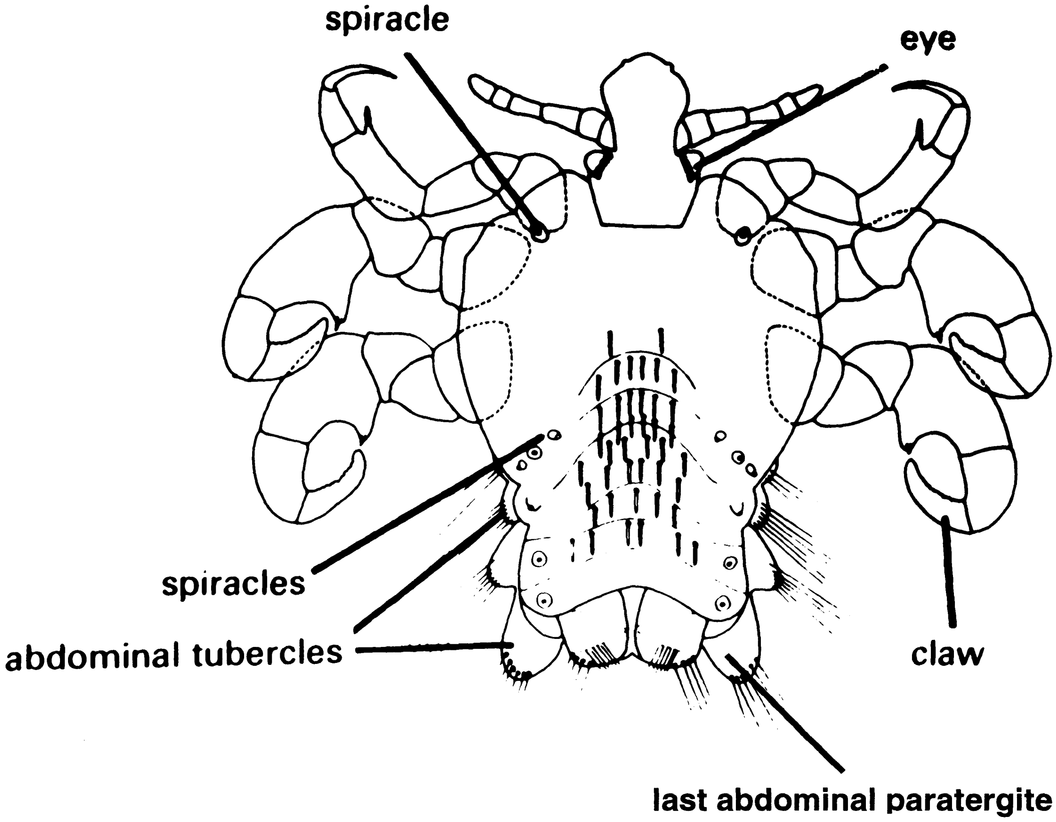


Figure 165. Dorsal view of *Pthirus pubis,* with principal parts labeled. From Kettle (1984), reprinted by permission of Chapman and Hall, United Kingdom.

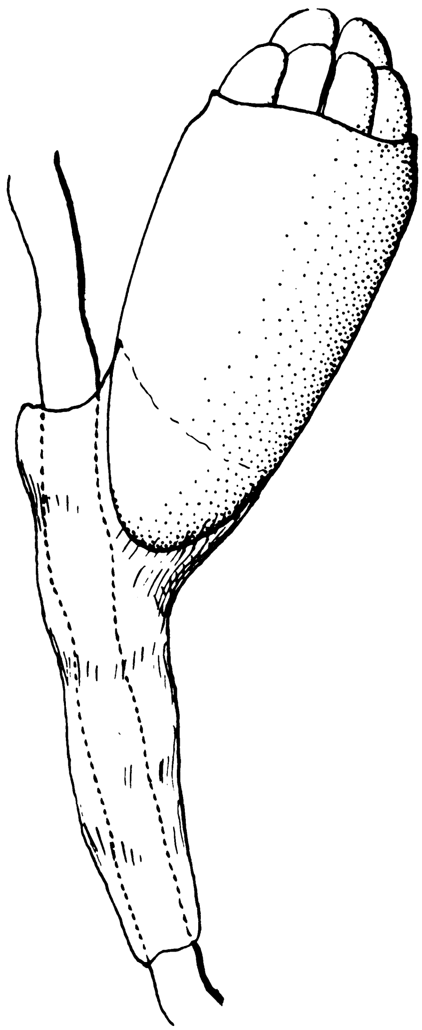


Figure 166. Egg of *Pthirus pubis* attached to a hair. From Ferris (1951), reprinted by permission of Pacific Coast Entomological Society.

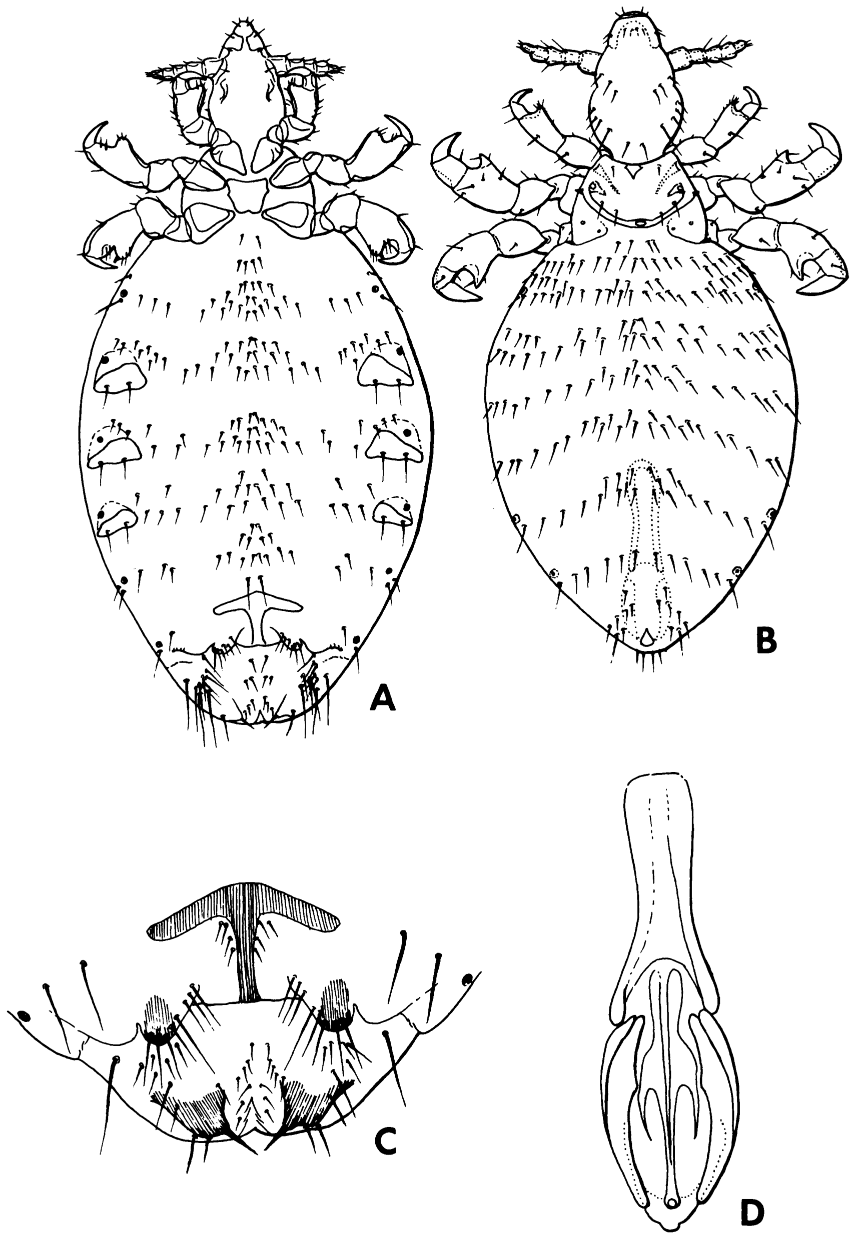


Figure 167. *Ratemia squamulata*: ***A***, Ventral view of female; ***B***, dorsal view of male; ***C***, female terminalia; ***D***, male genitalia. Redrawn with minor modification by Jan Read from Ferris (1951); courtesy of Pacific Coast Entomological Society.

LICE CONTROL

The practice of controlling lice by treating their hosts with insecticides can be conveniently divided into six chronological phases: (1) Prior to 1920, a large variety of home remedies were used, such as creosol, calomel and other mercury compounds, and petroleum derivatives. (2) Beginning in about 1920, there was a gradual shift to the use of sodium fluoride, nicotine sulfate, rotenone, and pyrethrum sprays and dusts. (3) Starting in about 1945, a series of synthetic compounds replaced the botanicals and other older chemicals. First DDT and soon afterward other chlorinated hydrocarbons (CH) were the insecticides of choice. (4) Beginning about 1955, organophosphorus (OP) compounds such as malathion and carbamates such as carbaryl came into use. (5) In about 1965, the synthetic pyrethroids (SP), pheromones and other attractants, and insect hormones became available. (6) Starting in about 1980, the fermentation products such as ivermectin and other sophisticated control chemicals were introduced and were often used in conjunction with nonchemical control measures under the heading of insect pest management. Obviously, these phases of louse control overlap each other.

In the 1990's, chemical control is often combined with cultural, biological, genetic, and other control measures to prepare an insect pest management (IPM) program that will reduce populations of pests to a point below the economic level. Among other considerations, IPM has the advantage of minimizing the application of chemicals and delaying the insecticide resistance problems that follow the repeated use of a particular insecticide or class of insecticides. But Axtell and Arends (1990) pointed out that in current poultry production, it is important to eliminate an ectoparasite as soon as it appears and not wait until a pest population reaches the economic threshhold.

In the following text, the control of lice on poultry has been separated from that on domestic animals and humans, even though many insecticides may be used for both purposes. But the methods of application, concentrations, formulations, or intervals between application often differ.

CONTROL OF LICE ON DOMESTIC ANIMALS

Before about 1920, many of the home remedies for louse control on cattle, sheep, goats, and other domestic animals were chemicals that were also used to control ticks, sheep keds, and other parasites of livestock. Greases (lard, axle grease) or oils (cottonseed, linseed, whale, or petroleum oil) were applied to cattle with a rag or brush. Lard was often fortified by mixing it with creolin, calomel, carbolic acid, coal tar, creosote, or other chemicals that killed lice. Mercurial ointment was commonly used, even though it sometimes burned the animal. The spray application of a dilute kerosene emulsion (Lamson 1918) was probably more effective than smearing a lousy animal with grease. Arsenical solutions, either homemade or proprietary, that were in common use for tick control were also applied to cattle and other domestic animals as washes, sprays, or dips to control both chewing and sucking lice. These home remedies may have been used for hundreds of years or, more likely, they were things that were at hand on the farms of the 19th century. Unfortunately, some of these materials were also skin irritants that would injure the animal unless applied sparingly and with care (Munro and Telford 1943).

The antiquity of these home remedies was attested to by Buckland and Perry (1989), who wrote, "The first century Roman poet Virgil refers to the smearing of a mixture of oil-lees, bitumen, pitch, sulphur, wax and various plant extracts onto the animal (Georgics, III 448–451) and his near contemporary, the agricultural writer Columella, not only provides many detailed recipes but also recommends dipping in a saline solution (Columella VII, 5–10)."

Cattle Lice

Sodium fluoride and sodium fluosilicate were recommended for cattle louse control by researchers such as Bishopp and Wood (1917a) and Shull (1932). Whether applied as a spray or a dust, they seem to have been more effective against cattle biting lice than sucking lice. Dusts were used most often in winter to avoid chilling the animals. Pyrethrum dusts were recommended, but they were more expensive than other insecticides and several applications were required. When combined with piperonyl butoxide or some other synergist, pyrethrum became more effective (Snipes 1948).

Sulfur, usually applied as finely ground flowers of sulfur, was a carrier for other insecticides that improved their efficacy. For example, a combination of nicotine sulfate and sulfur was used in dipping vats, where it was quite effective when used at a strength of 0.05% actual nicotine and maintained at 32–35 °C (Babcock and Cushing 1942a).

Munro and Telford (1943) found that of several dusts tested, a 1% nicotine-sulfur dust was the most efficient for control of the shortnosed cattle louse, longnosed cattle louse, and cattle biting louse. Rotenone was probably the most widely used insecticide for louse control during this era; either derris or cubé that contained 5% rotenone was diluted with sulfur and the mixture was applied as a dust or used as a dip (Wells et al. 1922, Babcock and Cushing 1942a, Hixson 1946, Matthysse 1946).

All insecticides in use before 1945 had the major disadvantages of not being ovicides and of not being very persistent (little or no residual activity). As a result, it was important to apply them two or three times at intervals of 14–21 days to eliminate lice that hatched after the cattle were treated.

Beginning in 1945, DDT was widely used to control cattle lice. It was applied as a dust, wash, spray, or dip, but beef cattle were most often sprayed in small pens with the animals being moved about so that the operator could spray first one side and then the other of each animal (fig. 168). Soon after DDT was marketed, several other CH's came into use to treat livestock (Lancaster 1951); probably the most widely used was toxaphene. Wells and Barrett (1946) found that 100% of eggs of the shortnosed cattle louse, as well as the lice, were killed by spraying cattle with 0.1% gamma isomer of benzene hexachloride. Furman (1947) reported eradication of sucking and chewing lice with one application of benzene hexachloride at a strength of 0.036% gamma isomer. Sprays were more effective for cattle lice control than dusts, and Williams (1992a) listed 10 insecticides that could be applied as a spray. TDE and chlordane were also widely used (Smith and Roberts 1956). Brown (1951) summarized information about lice control with synthetic insecticides during 1945–50.

Beginning in about 1955, several OP insecticides were tested as livestock treatments and some were effective for louse control. One of the more widely used was malathion, which was shown by Lancaster (1957) and DeFoliart (1957) to be ovicidal as well as insecticidal and to be highly effective against the shortnosed cattle louse (Smith and Richards 1955).

Other OP's, such as coumaphos and ronnel, were effective systemically and killed both lice and cattle grubs (DeFoliart et al. 1958), and the application of one spray for both pests became a common practice. The "pour-on" or "spot-on" application of OP insecticides [for example, ronnel, coumaphos, famphur (Rich 1966), fenthion, and chlorpyrifos (Loomis et al. 1976)] was also quite effective against cattle grubs and lice. Cattle chewing lice, which were not always killed by systemic insecticides, were eliminated by a pour-on application of crufomate (Meyer and Carey 1977).

Liebisch (1986) reported the effectiveness of flumethrin (Bayticol 1% pour-on), a synthetic pyrethroid, for control of sucking and chewing lice, with the chewing louse being more susceptible. Permethrin as both a pour-on and a spray and fenvalerate as a spray were recommended for louse control in Nebraska by Campbell (1992b). A permethrin pour-on was suggested by Mock (1990), who said that it gave excellent control of chewing lice but was less reliable for sucking lice. But Grisi et al. (1993) soon reported that cattle chewing lice in Rio Grande do Sul, Brazil, were resistant to SP's.

Injectable ivermectin and other fermentation products are very effective for control of blood-sucking lice but not the chewing louse (Losson 1990, Williams 1992a), and the numbers of chewing lice may increase in a treated herd. A pour-on formulation of ivermectin has become available that should improve control of the chewing louse (Campbell 1992a). Doramectin, another fermentation product, was shown by Logan et al. (1993) to completely eliminate three species of sucking lice and to reduce the number of cattle chewing lice by 82% after 28 days. They combined data from 16 studies which showed that doramectin was 100% effective after 7 days against sucking lice when cattle were treated at the rate of 0.2 mg/kg body weight with a 1% doramectin solution administered subcutaneously.

A 0.5% formulation of moxidectin, another fermentation product, was found to eliminate cattle chewing lice and long-nosed cattle lice when applied as a pour-on at 0.5 mg/kg (Losson and Lonneux 1993). The little blue cattle louse, *Solenopotes capillatus*, was eliminated from cattle treated orally with a slow release bolus of moxidectin after about 6 wk. When administered by subcutaneous injection, it acted faster; all lice were killed at 2–27 days posttreatment (Webb et al. 1991). Abamectin, a near relative of ivermectin, controlled sucking lice but not the cattle chewing louse (Heinz-Mutz et al. 1993).

Geden et al. (1990) and Lang (1992) found that cattle biting lice populations were sharply reduced on calves housed in individual hutches to isolate them from the spread of diseases and that the application of insecticides to those calves was usually unnecessary.

Backrubbers (usually a burlap-wrapped cable or heavy wire loosely suspended between two posts), which are used to control horn flies in summer, are also useful for wintertime control of cattle lice (fig. 169). Hoffman (1954a,b) found that if backrubbers are impregnated with relatively high concentrations of a general-purpose insecticide (such as 5% DDT or toxaphene), then control of the longnosed cattle louse and the cattle biting louse is usually adequate on all cattle that use the backrubbers. Bolte (1992) pointed out that backrubbers should be used to prevent louse infestation rather than to control a well-established infestation.

Gressette and Goodwin (1956) added 0.5% lindane and 2% or 5% malathion to the list of insecticides that could

Figure 168. Pen spraying of cattle, a common practice during the 1950's. Any of several chlorinated hydrocarbons or organophosphorus insecticides was applied for control of lice and other ectoparasites.

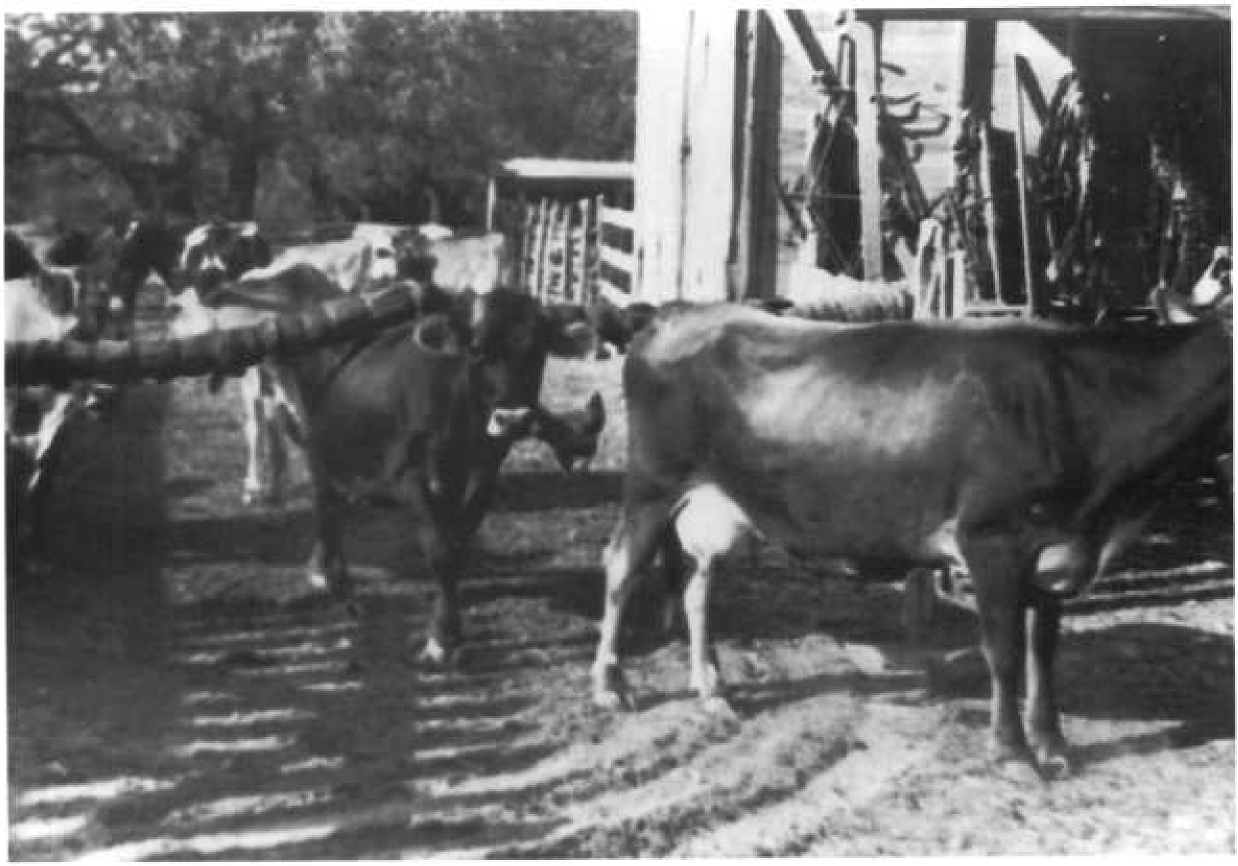


Figure 169. Self-treatment for louse control. By walking under a back rubber, cattle obtained enough insecticide to control lice as well as horn flies and other pests.

be applied with a backrubber. Williams (1992a) reported adequate louse control with backrubbers in Indiana if they were made available in late fall and were charged with 2% malathion or 1% coumaphos in mineral oil.

The cattle tail louse is more difficult to control than other cattle lice because it usually infests the coarse hair of the tail switch, a part of the body that is hard to spray. However, Creighton and Dennis (1947) and Bruce (1947) found that DDT was effective at concentrations of 1.5% or 2%. Some owners dipped only the tail of their cattle in a pail of concentrated insecticide.

To control lice on dairy cattle, only insecticides that will not be secreted in their milk can be used. Savos (1974) recommended the application of sprays containing crotoxyphos, or a combination of crotoxyphos and dichlorvos, or coumaphos.

The chemical control of cattle lice was reviewed by Losson (1990).

Sheep and Goat Lice

Chewing and sucking lice on sheep and goats were controlled in much the same way as cattle lice up to the mid-1930's. But then Babcock (1936) and Babcock and Cushing (1942b) found that goats and sheep (but especially Angora goats) were more effectively treated for louse control by dipping them in a suspension of finely ground sulfur or sulfur and rotenone.

After the CH insecticides came into general use, several of them (for example, DDT, toxaphene, chlordane, or lindane) were recommended for louse control in sheep and goats (Knipling 1952, Peterson and Bushland 1956). DDT and most other CH's are no longer available in the United States, but methoxychlor is still in use (Mock 1991). CH insecticides were effective as either sprays or dips, but dipping was gradually discontinued because it was laborious, there was greater risk of injuring animals, and the rather large quantity of insecticide required to fill a dipping vat made dipping quite expensive.

After goat lice became resistant to toxaphene and other chlorinatated hydrocarbons (Moore et al. 1959), those insecticides were replaced by OP insecticides such as malathion and diazinon. When sprayed on naturally infested goats at a concentration of 0.3%, malathion gave 99% control of a mixed infestation of chewing and sucking lice in Uttar Pradesh, India (Pandita and Ram 1990). Spraying or dipping of the entire animal was replaced with easy-to-apply pour-ons or spot-ons of fenthion, famphur, and other OP insecticides (Fuchs and Shelton 1985, Miller et al. 1985).

In South Africa, Baker (1969) found that the blue louse (*Linognathus africanus*) was resistant to the OP insecticide dioxathion. However, those same resistant strains were controlled satisfactorily with two other OP insecticides: dichlorfenthion and chlorfenvinphos.

Hall (1978) found an SP, cypermethrin, to be highly effective for control of the sheep biting louse when sheep were dipped in concentrations that varied from 1 to 10 ppm. The highest concentration provided 19 wk of protection against reinfestation. Heath and Bishop (1988) reported that a cypermethrin pour-on was slow in its action but had reduced the number of sheep biting lice by about 95% on day 48 of their test.

Himonas and Liakos (1989) used a pour-on of cypermethrin (Ectopor) at the rate of 1 ml/5 kg body weight, which provided 100% protection against goat biting louse and two species of sucking lice of goats for 28 days and almost 100% for 56 days. In their test, infested, untreated kids mingled with the treated animals for the entire test period. Levot and Hughes (1990) reported that the sheep biting louse did not appear to be resistant to cypermethrin in laboratory tests in Australia and that widespread reports of failure of a pour-on may have been due to inadequate treatment.

In 1991, Mock included fenvalerate and permethrin in his list of insecticides that can be applied to sheep and goats except that fenvalerate cannot be used on lactating milch goats. Dumanli et al. (1992) found that 100% of *Linognathus africanus* were controlled with fenvalerate and flumethrin (two SP's tested in vitro in Turkey) and 90%–100% were controlled with amitraz, a foramidine compound. In Western Australia, Morcombe et al. (1992) and Morcombe and Young (1993) reported that failure to eradicate the sheep biting louse with SP's was in part due to deficiencies in the application procedures and also in part to low-level resistance of the lice to cypermethrin, deltamethrin, cyhalothrin, and other SP's.

James et al. (1993) tested for resistance in vitro by using a treated surface technique and found that populations of South Australian sheep biting lice had developed resistance to cypermethrin in the range of 1 to 20 times (1–20×). In one sheep flock from Kangaroo Island, a resistance factor of 91× was found. Keys et al. (1993) found that many sheep biting lice survived the sheep being dipped in 20 ppm of cyhalothrin and 40 ppm of alphamethrin but that lice of the same populations did not survive dipping in 100 ppm of the OP insecticide diazinon.

The goat sucking louse was controlled with a single subcutaneous injection of ivermectin at a rate of 0.1 mg/kg body weight (Shastri 1991). The sheep biting louse was controlled with ivermectin sprays of 0.03 mg/ml of water applied with a jetting gun; this treatment gave 99% control in 15 wk (Cramer et al. 1993).

Rugg and Thompson (1993) described an in vitro assay that could be used to approximate the susceptibility of the sheep biting louse to avermectins (a group of fermentation products that includes ivermectin).

Drummond et al. (1992) found that certain strains of *Bacillus thuringiensis* were 10–20× more toxic to the sheep biting louse than were other strains. This suggests that the insecticidal qualities of *B. thuringiensis* have been substantially improved since the time that Gingrich et al. (1974) reported only partial control of two species of chewing lice of Angora goats and one of sheep with the products available at that time.

The insect growth regulators (IGR's) diflubenzuron and hydroprene successfully inhibited edysis (= control) in third-instar nymphs of the Angora goat biting louse (Chamberlain et al. 1976, Hopkins and Chamberlain 1978). In their research, the LC_{50} (ppm necessary to produce 50% inhibition of ecdysis) for third instars fed a treated diet for 6 days was 0.6 ppm. The topical application of another IGR, juveth, caused premature molts, supernumerary molts, and morphological changes in early third-instar nymphs (Hopkins et al. 1970, Chamberlain and Hopkins 1971). Other IGR's and juvenile hormone materials were sprayed onto infested goats, where they caused considerable but not complete mortality of lice.

Hopkins and Chamberlain (1980) exposed the eggs of the sheep biting louse to gamma radiation and found that susceptibility decreased as age of the egg progressed up to 8.5 days. Many of the male lice reared from these treated eggs had malformed testes, and the fecundity of females was reduced.

Hog Lice

A number of petroleum and vegetable oils were long relied on to control the hog louse. Simple homemade devices such as burlap sacks wrapped around a post in a hog pen and soaked with crude oil were effective rubbing posts that hogs used to control their own lice. Stevenson (1905) noted that undiluted kerosene, kerosene emulsion, creolin solution, kerosene emulsion plus pyrethrum, and kerosene mixed with cottonseed oil or raw linseed oil had been used successfully to control the hog louse. In addition, Metcalf and Flint (1928) stated that a mixture of equal parts of kerosene and lard could be applied directly to infested animals with a swab or brush. Also, hogs were dipped by running them through a shallow vat containing water and a surface layer of crude oil or a 1% solution of pine tar. Moore (1947) found that a white mineral oil solution of pyrethrum plus piperonyl butoxide was 100% effective when applied along the backline at the rate of 3/4 oz of solution per grown animal. Two applications at a 14-day interval were required. The same solution could be applied to a rubbing post.

Any of several CH insecticides were recommended by Cobbett and Bushland (1956), but later work showed that OP's were even more effective for control of hog lice. Stirofos (Butler 1973), ronnel (DeWitt 1975), fenthion, and malathion (Collison 1978) are only a few of the many OP's recommended. Collison recommended three CH insecticides and seven OP's for application as a spray, pour-on, or dust. McGregor and Gray (1963) reported that hog lice had been controlled by placing 5% ronnel granules in the bedding sometimes used in farrowing houses. Knapp et al. (1977) said that fenthion applied by the spot-on technique gave excellent control of hog lice.

In 1982 USDA recommended three CH and nine OP insecticides for hog louse control, applied as conventional sprays, mist sprays, dips, pour-ons, or dusts, or applied to a hog rubber (Drummond 1982). Malathion sprays at a 0.25% or 0.5% concentration eliminated hog louse infestations for 9 days but not for 35 days; apparently some eggs survived both treatments (Johnson 1958).

When used for hog louse control as sprays, the SP's permethrin and fenvalerate were quite effective (McKean et al. 1992, Nolan 1988), as was ivermectin at the rate of 0.3 mg/kg body weight. McKean et al. and Williams (1992c) suggested 12 insecticides for louse control that had been approved for application to hogs. They were two CH's, six OP's, two SP's, one fermentation product, ivermectin, and a foramidine compound, amitraz. If the goal is louse eradication, they recommended the use of 0.3 mg/kg body weight of ivermectin as an injection, with great care taken to ensure that every hog on a premise is treated and that the swine herd is maintained in isolation.

Lice On Horses

The control of ectoparasites of horses must be undertaken with special care because of difficulties of application, animal size, high dollar value of horses, and other considerations. Nevertheless, historically, horses have been treated with many of the same insecticides that are applied to other livestock, but are more apt to be sponged, brushed, or dusted than treated with a power sprayer or dipped.

For control of the horse biting louse, Metcalf and Flint (1928) recommended sodium fluoride dusts, or 2%–3%

cresol in water as a wash, or a proprietary coal-tar dip, or rubbing with raw linseed oil. Sodium fluoride is ineffective for control of the horse sucking louse, but the other materials were used. To the list of insecticides, Cameron (1932) added sprays and washes of nicotine sulfate at a strength of 0.05-% actual nicotine.

Cress (1975) found that lice on horses were controlled by either a 0.75% spray or a 4% dust of malathion or a spray of 0.06%–0.12% coumaphos. Heusner et al. (1991) recommended that 0.06%–0.125% coumaphos or 0.3% permethrin be used to control both kinds of horse lice. The synthetic pyrethroids may control lice with only one application (Knapp 1985).

Foil and Foil (1990) stated that the horse sucking louse is easily controlled by treating the horse with ivermectin.

Bolte and Coppock (1991) and Campbell (1992b) pointed out that horses have sensitive skin and are more easily burned by the solvents in emulsions of an insecticide than are other livestock. The horse owner should not purchase a livestock spray unless its label specifically states that it can be applied to horses.

CONTROL OF LICE ON SMALL ANIMALS

Numerous insecticides have been used to control lice on dogs and cats, but it is important to avoid materials that might injure the host. Cats are especially susceptible to insecticide poisoning because of their habit of frequently cleaning themselves with their tongue. Rotenone and pyrethrum dusts have been extensively used, especially on cats, because of their low mammalian toxicity.

For dogs, Kim et al. (1973) suggested dusts of 5% DDT, 5% methoxychlor, 5% chlordane, or 1% lindane. Or dogs can be sprayed with 0.5% DDT, 0.5% methoxychlor, 0.5% chlordane, or 0.025% lindane. Dogs are highly sensitive to toxaphene, so it should not be applied to them. Cats should not be treated with DDT or lindane because they are especially susceptible to poisoning with those insecticides; otherwise, treatment is the same as that for dogs.

Sosna and Medleau (1992c) emphasized the need to correct the underlying causes of massive louse infestations of dogs and cats: malnutrition, anemia, overcrowding, and poor hygiene and sanitation practices.

Laboratory colonies of rats and mice sometimes harbor large numbers of the spined rat louse and a louse from mice, *Polyplax serrata*. To eliminate an infestation, it may be necessary to steam-clean cages and rooms, burn all litter, and treat the animals with an insecticide.

Heston (1941) recommended sprays of sodium fluoride or pyrethrum to control lice on laboratory mice. Dipping is less satisfactory because mice often become chilled after dipping and may develop pneumonia.

Buxton and Busvine (1957) stated that the simplest effective method of control for chewing and sucking lice on laboratory animals is to dust all affected animals using derris powder (1% rotenone) or pyrethrum powder (0.5% pyrethrins). DDT, as a 5% dust, was also recommended. After treating the animals, a little insecticide should be applied to the bedding. Woodnott (1963) stated that pyrethrum, rotenone, DDT, and lindane had been widely and successfully used for louse control on laboratory animals.

Tuffery and Innes (1963) recommended dusts of lindane, pyrethrum, or—if applied sparingly—DDT. For louse control on laboratory rats and mice, Kim et al. (1973) stated that insecticidal dusts should be applied weekly for 2–3 wk.

Use of the following insecticides was suggested by Kim et al. (1973): 0.5%–1.0% rotenone, 0.05%–0.1% pyrethrins, 0.25%–0.5% lindane, or 3%–5% malathion. They preferred dusts, but sprays and dips of 0.1%–0.25% methoxychlor or 0.03%–0.06% diazinon could be used. For rabbits only, they suggested dusts of 1%–2% chlordane or 10% trichlorfon.

CONTROL OF HUMAN LICE

As happened with lice of domestic animals and poultry, the treatment of humans to control parasitic lice was at one time a matter of using home remedies—the simple substances at hand (Waterston 1921, Metcalf and Flint 1928, Lindsay 1993). For head lice, they said that a person's head could be treated with a mixture of equal parts of kerosene and olive oil, followed in an hour or two with a shampoo using warm water. Or the hair could be soaked for 15 min in a solution of 12 grains (about 0.8 g) of carbolic acid crystals in a pint of water. The wet head was wrapped in a cloth for another hour before shampooing out the carbolic acid. The application of a paraffin oil (= kerosene) emulsion containing at least a 30% active ingredient, followed by a bath with hot water and soap, was relied on in Great Britain, according to Waterston. The addition of 5% of one of the essential oils, such as sassafras or eucalyptus oil, increased the toxicity of the emulsion. Vinegar was used to dissolve the cement with which the egg was attached, and then the nits (eggs) could be easily brushed off the hair. Lindsay described louse control in Glasgow, Scotland, over 100 yr ago; infested persons used a wide variety of remedies, including the herbals (*Delphinium*, quassia chips, sebadilla, leaf tobacco, chrysanthemums, etc.), inorganic treatments such as mercury compounds, and others (vinegar, phenols, and essential oils). For body lice and crab lice, blue (or mecurial) ointment or tincture of larkspur (a plant in the genus *Delphinium*) were widely used before 1940.

During World War II, USDA's Agricultural Research Service searched for improved control measures for human lice. An outstanding wartime accomplishment was the formulation of MYL powder, which contained pyrethrins (Bushland et al. 1944b). The formula for MYL powder is as follows:

	Percent
Pyrethrins (from a 20% concentrate)	0.2
In-930 (synergist)[a]	2.0
2,4-dinitroanisole (ovicide)	2.0
Phenol S (antioxidant)[b]	0.25
Pyrophyllite to make 100%	

[a] N-isobutylundecylenamide

[b] Essentially isopropyl cresols

Dosage was 30 g/underwear suit. The powder was also effective against head lice and crab lice.

About 2 yr after the development of MYL powder, it was replaced by DDT, a simpler, easy-to-use insecticide. DDT was applied to the clothing and bodies of people infested with the head louse, body louse, or crab louse and also to prevent infestation. It was especially effective when clothing was impregnated with a solution or an emulsion of DDT, because clothing remained toxic to lice even after it had been laundered five times. To impregnate clothing, an emulsion concentrate of DDT was diluted with water to make an emulsion that contained 1%–2% DDT; then the clothing was dipped in the emulsion and wrung out to dry. Also, solvents ordinarily used in dry cleaning could be used to dissolve DDT; then the clothing was treated with that solution (Bushland et al. 1944a).

The NDIN formula was another ARS development that was used to control head lice and crab lice (Eddy and Bushland 1946). It consisted of the following:

	Percent
Benzyl benzoate	68
Tween 80 emulsifier	14
Benzocaine	12
DDT	6

The concentrate was emulsified in 5 parts of water and applied to the head. NDIN killed all stages of head lice, including the egg, and could be used to control crab lice.

In 1950 Eddy (1952) found that body lice on prisoners held on Koje Island, Korea, were resistant to 10% DDT, but the lice were susceptible to lindane and other CH insecticides and to pyrethrins. As a result, DDT was replaced by a 1% lindane dust for louse control in the armed forces of the United States; but by 1954, body lice were also resistant to lindane. Under intense pressure in the laboratory, a strain of body lice did not develop resistance to malathion (Cole et al. 1969), but formulations of malathion were too malodorous to be widely accepted for application to humans. Also, some resistance to malathion did develop in time. Body lice that were 37× resistant to malathion were found in Burundi, Africa, but when they were reared without exposure to malathion, this strain lost most of its resistance. When again pressured in the laboratory, 4× to 8× resistance was recorded (Cole et al. 1973). Mumcuoglu et al. (1990a) did not find resistance to malathion in head lice collected in Israel.

Malathion was believed to be an ovicide during the early years of its use, but Burgess (1991) found that not all formulations of malathion were equally effective as ovicides. The better ovicides contained excipients that assisted penetration of the louse egg by the malathion.

Mathias and Wallace (1990) tested proprietary lousicides of lindane (Kwellada) and pyrethrins (R & C shampoos) as ovicides for the head louse. Since both permitted over 50% hatch of nits, this treatment would have to be applied twice at about 7-day intervals to free people of head lice. The lindane lotion Kwell is not recommended by the National Pediculosis Association because lice may be resistant to lindane, it is a more toxic insecticide, and it is slower in its action (Evans 1991).

Mumcuoglu and Miller (1991) found that a spray of 0.66% pyrethrins and 33% isododecane killed 100% of body lice and 99% of their eggs. (For convenience, they used body lice to test formulations used for control of head lice, based on their earlier report that body lice are more susceptible than head lice to insecticides.) They also tested 14 proprietary head-lice remedies against body lice. A gel and any of the solutions of carbaryl, malathion, and pyrethrins were more effective than shampoos, except one shampoo that contained 1% malathion and killed 100% of motile lice but only 12.8% of eggs. A lotion of 0.5% malathion was more effective; it caused 100% mortality of body lice and 85% of eggs. In other tests by Mumcuoglu et al. (1990c), body lice were highly susceptible to the SP's deltamethrin and permethrin, both of which are used for louse control in some countries.

Mumcuoglu et al. (1990a,c) used in vitro tests to find that 81%–100% of body lice died after feeding on blood that contained 2.5–10 ng of ivermectin per ml. From their in vivo tests with rabbit hosts for body lice, they found that ivermectin was toxic to human body lice that fed on treated rabbits for 2–3 days posttreatment; but mortality then declined. Mortality in lice that fed on treated rabbits at 6 days posttreatment was no higher than mortality in lice that fed on untreated rabbits.

Dunne et al. (1991) found that the percentage of children with head lice in a Sierra Leone, Africa, village who had been treated with a single oral dose of ivermectin for the control of onchocerciasis was about half that of a comparable group of untreated children.

Rabbits, which are used as hosts for laboratory colonies of body lice, were partially immunized by Ben-Yakir et al. (1994) by injecting them with an extract of louse midgut. Lice that fed on treated hosts ingested less blood, had a higher mortality, and laid fewer eggs than did lice that fed on untreated hosts.

Burgess (1993) suggested that a repellent for head lice would be useful to supplement insecticides because in living areas where only a few head lice are present, uninfested persons could use a repellent to protect themselves from lice.

CONTROL OF POULTRY LICE

Poultry with large numbers of lice may be lethargic, fail to feed adequately, lose their feathers, and in general appear unhealthy. Since poultry lice ordinarily remain on their hosts constantly, the birds themselves must be treated in order to free them of lice. Until about 1920, one of the most popular control measures was to apply one of several greases or ointments. For example, Schoppe (1917) suggested that baby chicks be treated by rubbing hog lard on the head and under the wings. Older birds were treated with a mixture of 1 part mercurial ointment and 2 parts petrolatum; a pea-sized portion was placed under each wing and near the vent. Bishopp and Wood (1917a) commented that mercurial ointment was effective against the chicken body louse but not the chicken head louse or the wing louse. Poultry were also dusted with powdered sulfur or a mixture of crude carbolic acid and plaster of paris (Pierce and Webster 1909). Another dust was prepared by diluting 1 part of 90% crude carbolic acid with 8 parts of cold water and then sprinkling it on lime (Banks 1907). The natural tendency of chickens to dust themselves by wallowing in wood ashes or dusty earth was exploited by providing dust boxes in the poultry yard. These dust baths contained powdered sulfur, tobacco powder, or mixtures of some of the previously mentioned insecticides with wood ashes or some other diluent.

Banks (1907) wrote that hens are usually able to keep lice (and mites) in check by dusting themselves, but that setting hens may be infested with enormous numbers of these parasites (since they do not leave the nest to dust themselves). Young chicks hatched by these hens may be so severely attacked that they are killed by the lice.

Soon after the effectiveness of fluorine insecticides was reported, they rapidly came into general use for the control of poultry lice. Herms (1939) stated, "No remedy has given such uniformly satisfactory results in the control of lice of domesticated birds as has sodium fluoride (NaF), apparently first used against these parasites by Bishopp and Wood in 1917."

During the period 1920–46, most writers on the subject recommended the application of either sodium fluoride or sodium fluosilicate as a dust or dip. Dusts were applied by the "pinch" method; about 10 pinches of the sodium fluoride powder were placed on different parts of the fowl's body. If the poultry raiser preferred, the powder could be applied with a shaker can. Sometimes the sodium fluoride was diluted with 2 parts of finely ground sulfur. Because of its coarseness, sodium fluosilicate was seldom used as a dip. Dusting by the pinch method was tedious and many poultrymen preferred to dip their birds, especially if large numbers needed to be treated. The dip was prepared by dissolving or suspending 1 oz of sodium fluoride powder in 1 gal of tepid water.

Another dip was prepared by mixing 1 part of Zenoleum (cresol from coal tar distillation) with 50 parts of water (Schoppe 1917). The application of blue ointment was included in the recommendations of Kinghorne and Green (1920). This remedy contained about 9%–11% mercury (often in the form of mercury oleate) in anhydrous lanolin, white petrolatum, or some other base. Wells et al. (1922) described the use of $\frac{1}{4}$ oz of powdered derris root per gal of water to control poultry lice.

At the end of World War II, the synthetic insecticides became available and rapidly replaced the fluorines. Alicata et al. (1947) found that a 3% DDT dust was effective against the chicken body louse. Benzene hexachloride in petroleum oil solution was found by Telford (1947) to control three species of poultry lice when sprayed on the roost or floor of poultry houses. However, off-flavored eggs and poultry meat were caused by treatment with benzene hexachloride (mixed isomers); so it was soon replaced by lindane, the gamma isomer of benzene hexachloride, which has little or no odor. Hansens (1951) found that lindane was quite effective as a roost paint or as a spray on poultry litter. Hoffman (1956) reported that 1% lindane dust gave complete control of poultry lice. In addition to lindane, Smith (1952) found that chlordane sprays and

10% DDT dusts provided satisfactory control of the poultry lice.

Later the CH's were gradually replaced by the OP insecticides. Malathion was one of the more widely used OP's, but diazinon, coumaphos, dicapthon, ronnel, dimethoate, and naled were effective in various tests (Smith 1954; Hoffman 1956, 1960, 1961; Loomis et al. 1975a). Smith and Richards (1955) compared seven CH's with two OP insecticides for control of the chicken body louse. Motile forms were eliminated by all the insecticides, but the louse eggs must have been more resistant, because most of the treated birds were again lightly louse infested 2–4 wk after treatment. A 4% malathion dust placed in dust boxes protected birds from lice. Hoffman and Hogan (1967) found that if a 2% dust of phosmet or carbophenothion was applied to the litter in a chicken house, the hens would treat themselves.

Lice can often be eliminated by the fumigant action of volatile insecticides if they are applied to the roost or placed in some other way so that the birds are exposed to the vapors for prolonged periods. In addition to such older insecticides as nicotine sulfate and lindane, malathion controlled lice when applied as a roost paint. The fumigant action of dichlorvos was demonstrated by Kunz and Hogan (1970), who found that three species of chicken lice could be controlled by attaching resin strips impregnated with dichlorvos to the birds' legs or to the bottoms of layer cages.

Carbaryl was also effective for control of the common species of poultry lice. Although sometimes used as a spray, carbaryl was usually applied as a 4% or 5% dust (Hoffman 1960, Matthysse 1966, Kim et al. 1973). Also Matthysse suggested that small electric mist applicators could be used to thoroughly spray caged laying hens.

Axtell and Arends (1990) said that malathion, carbaryl, and stirofos are used for control of poultry lice but that permethrin is the most widely used. In addition to any of three OP insecticides or carbaryl, permethrin was suggested by Williams (1992b) for direct application to poultry, especially to floor flocks of laying hens or small farm flocks.

The fermentation product *Bacillus thuringiensis* was tested against the chicken body louse, shaft louse, and wing louse by Hoffman and Gingrich (1968). Action of the insecticide was slow, but when 4 g of a commercially prepared dust was applied to each hen, the louse numbers were reduced to zero at 28 days posttreatment.

In 1982, the only materials recommended by the U.S. Department of Agriculture (Drummond 1982) were carbaryl, carbaryl plus sulfur, coumaphos, malathion, stirofos, and a mixture of stirofos and dichlorvos.

The biological control of poultry lice is not yet widely used, but some research is in progress. An example is the control of the chicken body louse with the fungus *Trenomyces histophtorus*, which has been studied by Meola and DeVaney (1976) (fig. 170).

Arends and Stringham (1992) described an IPM program for poultry ectoparasites that (1) minimizes the use of insecticides and (2) emphasizes cultural practices that protect poultry from outside sources of lice and also monitors the flock to detect low-level infestations of lice. Williams (1992b) noted that lice are seldom found in modern, well-tended poultry flocks and are most often seen on birds in small farm flocks or on laying hens that are kept on the poultry house floor.

Wood (1922) recommended that sodium fluoride be applied to pigeons to control lice; it was used either as a dip to eradicate the lice or as a dust to control the lice. Loomis et al. (1975a) suggested dusts of 4% malathion or 5% carbaryl to control pigeon lice.

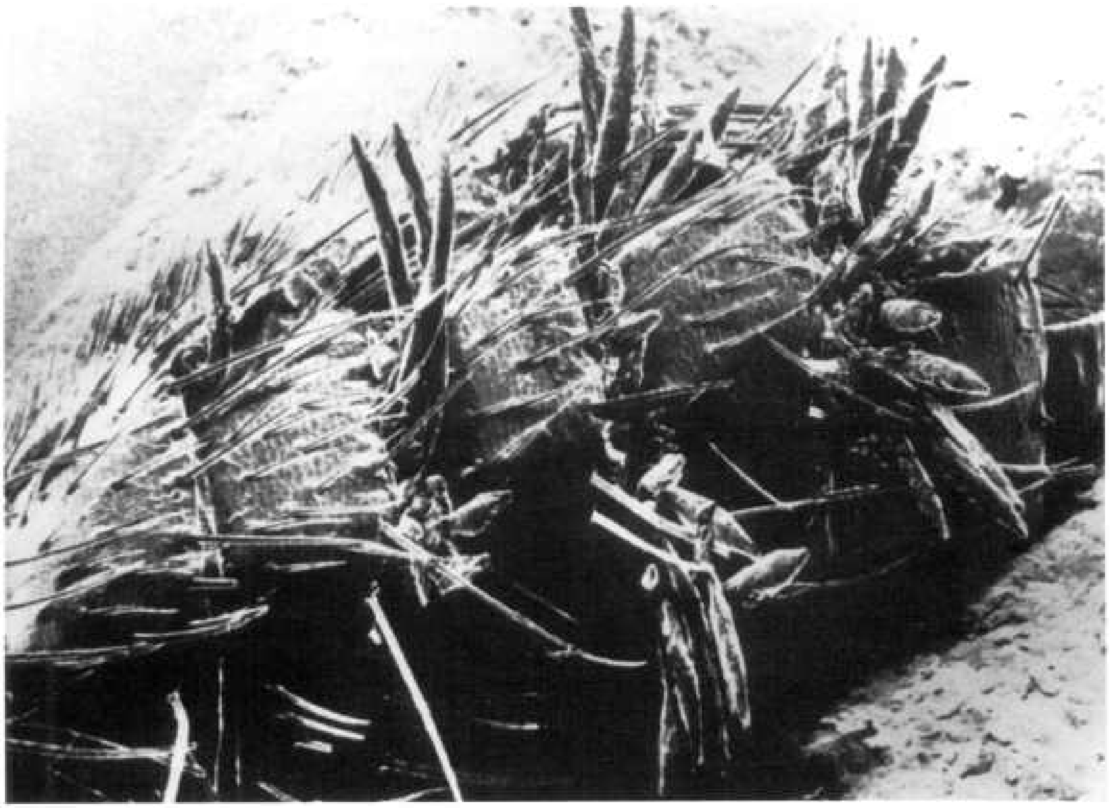


Figure 170. Biological control of *Menacanthus stramineus.* The apparent outward-projecting spines from the louse's body are perithecia of the fungus *Trenomyces histophtorus.* The perithecia have penetrated the exoskeleton at the nonsclerotized intersegmental sutures and are connected to the extensive rhizomycelium inside the insect's body. From Meola and DeVaney (1976), reprinted by permission of Academic Press Ltd, London.

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Appendix A. Hosts and distribution of lice in the order Mallophaga[a, b]

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution[c]: Louse	Distribution[c]: Host
Order Mallophaga, suborder Amblycera, family Abrocomophagidae					
Abrocomophaga chilensis[1] Emerson & Price	*Abrocoma bennetti*[1] Waterhouse	Abrocomidae[2]	Chinchilla rat[1]	Chile: Santiago (Til Til)[1]	Chile: Copiapo[3] to Rio Biobio
Order Mallophaga, suborder Amblycera, family Boopiidae					
Boopia bettongia[4] Le Souef	*Isoodon macrourus*[5] (Gould)	Peramelidae[5]	Brindled bandicoot[6]	Australia: Victoria, Queensland, New South Wales, Western Australia	Australia: New South Wales, Queensland, Northern Territory; New Guinea[2]
	Isoodon obesulus (Shaw)		Brown bandicoot		Australia: Queensland, New South Wales, Western Australia, Tasmania
	Perameles nasuta E. Geoffroy		Long-nosed bandicoot		Australia: Queensland, New South Wales, E. Victoria[3]
Boopia biseriata Kéler	*Macropus antilopinus* (Gould)	Macropodidae	Antelope kangaroo	Australia: Northern Territory, Western Australia	Australia: Queensland, Northern Territory, Western Australia
	Macropus robustus Gould		Wallaroo		Australia: All except Tasmania
Boopia doriana Kéler	*Dendrolagus dorianus* Ramsay		Doria's tree kangaroo	New Guinea	New Guinea: Interior
Boopia dubia Werneck & Thompson	*Lasiorhinus latifrons*[4] (Owen)	Vombatidae	Hairy-nosed wombat	Australia: South Australia	Australia: Queensland, South Australia, S.E. Western Australia
Boopia emersoni[7] Clay	*Dasyurus* (= *Satanellus*)[3] *albopunctatus* Schlegel	Dasyuridae[3]	New Guinean native "cat"	New Guinea: Papua (Star mts.)	New Guinea
Boopia grandis[4] Piaget	*Macropus fuliginosus* (Desmarest)	Macropodidae	Western gray kangaroo	Probably same as hosts	Australia: New South Wales, Victoria, South Australia, Western Australia
	Macropus giganteus Shaw		Great gray kangaroo		Australia: Queensland, New South Wales, Victoria, Tasmania
	Macropus rufus (Desmarest)		Red kangaroo		Australia: All, if habitat is suitable; endangered
Boopia greeni[8] Clay	*Antechinus minimus*[6] (Geoffroy)	Dasyuridae[6]	Little Tasmanian marsupial-mouse	Australia: Tasmania[8]	Australia: South Australia, Tasmania
	Antechinus swainsonii (Waterhouse)		Dusky marsupial-mouse		Australia: Queensland, New South Wales, Victoria, South Australia, Tasmania
Boopia minuta[4] Le Souef	*Macropus dorsalis*[3] (Gray)	Macropodidae	Black-striped wallaby	Awaits confirmation[4]	Australia: E. New South Wales, E. Queensland
Boopia mjobergi Werneck & Thompson	*Macropus giganteus* Shaw		Great gray kangaroo	Awaits confirmation	Australia: Queensland, New South Wales, Victoria, Tasmania

[a]Superscript numbers indicate references listed at end of appendix A. Where no superscript appears, the last number above applies.
[b]Where no item appears in a column, the last item above applies.
[c]Authors used current names for geographical entries in cols. 5 and 6. However, references for this appendix may use out-of-date geographical names.

Louse	Host			Distribution	
	Scientific name	Family	Common name	Louse	Host
Order Mallophaga, suborder Amblycera, family Boopiidae—*Continued*					
Boopia notafusca[4] Le Souef	*Wallabia bicolor*[3] (Desmarest)	Macropodidae[6]	Black-tailed wallaby[6]	Australia: Victoria, New South Wales[4]	E. Australia[3]
Boopia tarsata Piaget	*Vombatus hirsutus* (Perry)	Vombatidae	Coarse-haired wombat	Australia: New South Wales, Victoria, Tasmania	Australia: New South Wales[6]
	Vombatus ursinus (Shaw)		Common wombat		Australia: S.E. Australia,[3] Tasmania
Boopia uncinata Harrison & Johnston	*Dasyurus geoffroyi* Gould	Dasyuridae	Western native "cat"	Australia: Queensland, New South Wales, Western Australia, Northern Territory	Australia: Almost all; largest numbers in W. and S. Australia
	Dasyurus hallucatus Gould		Little northern native "cat"		Australia: Queensland, Northern Territory, Western Australia
	Dasyurus maculatus (Kerr) (not confirmed)		Tiger "cat"		Australia: Queensland, New South Wales, Victoria, South Australia, Tasmania
Heterodoxus alatus Kéler	*Thylogale brunii* (Schreber)	Macropodidae	Scrub wallaby[2]	New Guinea	New Guinea, Bismarck Archipelago[2]
Heterodoxus ampullatus Kéler	*Petrogale penicillata* (Gray)		Brush-tailed rock wallaby[6]	Australia: New South Wales	E. Australia: All except Tasmania[3]
Heterodoxus ancoratus Kéler	*Macropus parryi* Bennett		Whiptail or pretty-faced wallaby	Australia: Queensland	Australia: N.E. New South Wales, E. Queensland
Heterodoxus calabyi Kéler	*Wallabia bicolor* (Desmarest)		Black-tailed wallaby	Australia: New South Wales, Queensland, South Australia	E. Australia
	Macropus dorsalis (Gray)		Black-striped wallaby		Australia: E. New South Wales, E. Queensland
	Macropus eugenii (Desmarest)		Tammar		Australia: S.W. Australia, South Australia, coastal islands
Heterodoxus keleri[8a] Clay	*Dorcopsis vanheurni*[8a] Thomas		New Guinea forest mountain wallaby	New Guinea: Huon peninsula, Morobe[8a]	New Guinea
Heterodoxus longitarsus[4] (Piaget)	*Macropus giganteus*[5] Shaw		Great gray kangaroo	Probably same as host[4]	Australia: Queensland, New South Wales, Victoria, Tasmania
Heterodoxus maai Emerson	*Dorcopsis veterum* (Lesson)		New Guinea forest wallaby	New Guinea: West Irian	New Guinea, adjacent islands
Heterodoxus macropus Le Souef & Bullen	*Macropus agilis*[3] (Gould)		Sand wallaby	Australia: Queensland	N. Australia, New Guinea
	Macropus giganteus Shaw		Great gray kangaroo		Australia: Queensland, New South Wales, Victoria, Tasmania
	Thylogale stigmatica (Gould)		Red-legged pademelon		N.E. Australia, New Guinea
	Macropus rufogriseus (Desmarest)		Red-necked wallaby		Australia: Queensland, New South Wales, Victoria, South Australia, Tasmania
Heterodoxus mitratus[4] Kéler	*Dorcopsulus vanheurni*[3] (Thomas)	Macropodidae[6]	New Guinea forest mountain wallaby[6]	New Guinea: E. Papua (Mt. Mura)[4]	New Guinea[3]

Appendix A. Hosts and distribution of lice in the order Mallophaga—*Continued*

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host
Order Mallophaga, suborder Amblycera, family Boopiidae—*Continued*					
Heterodoxus octoseriatus Kéler	*Petrogale penicillata* (Gray)		Brush-tailed rock wallaby	Australia: New South Wales	Australia: All except Tasmania
Heterodoxus pygidialis (Mjöberg)	*Dendrolagus lumholtzi* Collett		Lumholtz's kangaroo	Australia: Queensland	Australia: N.E. Queensland
Heterodoxus quadriseriatus Kéler	*Setonix brachyurus* (Quoy & Gaimard)		Short-tailed scrub wallaby	Australia: Western Australia	S.W. Western Australia
Heterodoxus spiniger (Enderlein)	*Canis adustus* Sundevall	Canidae[3]	Side-striped jackal	Probably worldwide; recorded from all continents but Europe and Antarctica. More prevalent in tropical and temperate regions.	E. Africa, S. Africa
	Canis aureus Linnaeus		Golden jackal		N. and E. Africa, south to Senegal, Nigeria and Tanzania; SE Europe; S. Asia to Thailand
	Canis familiaris[9] Linnaeus		Domestic dog[9]		Worldwide[9]
	Canis latrans[3] Say		Coyote		North America, including Central[3] America
	Canis rufus Audubon & Bachman		Red wolf[10]		U.S.: S., C. states
	Urocyon cinereoargenteus (Schreber)		Eastern gray fox[9]		S. Canada, U.S., Mexico, Central America, to Colombia and Venezuela
	Genetta victoriae[11] Thomas	Viverridae	Giant genet[47]		Zaire, Congo[47]
	Civettictis civetta[3] (Schreber)		African civet		Subsaharan Africa to Somaliland and S. Africa[2]
	Macropis agilis (Gould) (not confirmed)	Macropodidae[4, 6]	Sand wallaby[6]		N. Australia, New Guinea[3]
Heterodoxus ualabati Plomley	*Wallabia bicolor* (Desmarest)		Black-tailed wallaby	Australia: Victoria, New South Wales, Queensland	E. Australia
Latumcephalum greeni[12] Clay	*Macropis rufogriseus* (Desmarest)		Red-necked wallaby	Australia: Tasmania (Green's Beach)[12]	Australia: Queensland, New South Wales, Victoria, South Australia, Tasmania
Latumcephalum lesouefi[4] Harrison & Johnston	*Wallabia bicolor* (Desmarest)		Black-tailed wallaby	Australia: Victoria, New South Wales,[4] Queensland	E. Australia
Latumcephalum macropus Le Souef	*Macropus dorsalis* (Gray)		Black-striped wallaby	Australia: Victoria	Australia: E. New South Wales, E. Queensland
Macropophila biarcuata Kéler	*Thylogale stigmatica* (Gould)		Red-legged pademelon	Australia: New South Wales, Queensland	Australia: N.E. Australia; New Guinea
	Thylogale thetis (Lesson)		Red-necked pademelon		Australia: Queensland, New South Wales
Macropophila breviarcuata[4] Kéler	*Thylogale stigmatica*[3] (Gould)	Macropodidae[6]	Red-legged pademelon[6]	Australia: New South Wales, Queensland	N.E. Australia, New Guinea[3]

Appendix A. Hosts and distribution of lice in the order Mallophaga—*Continued*

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host
Order Mallophaga, suborder Amblycera, family Boopiidae—*Continued*					
Macropophila clayae Kéler	*Thylogale billardierii* (Desmarest)		Tasmanian pademelon	Australia: Tasmania	Australia: S.E. South Australia, Victoria, Tasmania
Macropophila forcipata Mjöberg	*Thylogale stigmatica* (Gould)		Red-legged pademelon	Australia: Queensland	N.E. Australia, New Guinea
Paraboopia flava Werneck & Thompson	*Macropus robustus* Gould		Wallaroo	Australia: New South Wales	Australia: All except Tasmania
Paraheterodoxus calcaratus Kéler	*Petrogale penicillata* (Gray)		Brush-tailed rat-kangaroo	Australia: Western Australia[3]	Australia: All except Tasmania
Paraheterodoxus erinaceus Kéler	*Potorous tridactylus*[4] (Kerr)	Potoroidae[3]	Long-nosed rat-kangaroo	Australia: Tasmania	Australia: Almost all[4]
Paraheterodoxus insignis Harrison & Johnston	*Aepyprymnus rufescens* (Gray)		Rufous rat-kangaroo	Australia: New South Wales	Australia: Queensland, New South Wales, Victoria
Phacogalia brevispinosa Harrison & Johnston	*Antechinus bellus*[5] (Thomas)	Dasyuridae	Fawn marsupial-mouse	Australia: Northern Territory, New South Wales, Victoria, Tasmania	Australia: Northern Territory[3]
	Antechinus flavipes (Waterhouse)		Yellow-footed marsupial-mouse		Australia: Almost all
	Antechinus minimus (E. Geoffroy)		Little Tasmanian marsupial-mouse		Australia: South Australia, Tasmania
	Antechinus stuartii Macleay		Macleay's marsupial-mouse		Australia: E. Queensland, E. New South Wales, Victoria
	Antechinus swainsonii (Waterhouse)		Dusky marsupial-mouse		Australia: Queensland, New South Wales, Victoria, South Australia, Tasmania
Phacogalia spinosa Harrison & Johnston	*Phascogale tapoatafa* (Meyer)		Common wambenger	Australia: Victoria, Western Australia	All Australia, if habitat is suitable
Therodoxus oweni[8a] Clay	*Casuarius casuarius*[13] (Linnaeus)	Casuariidae[13]	Southern cassowary[13] (includes double-wattled cassowary)	New Guinea[8a]	New Guinea; Australia:[13] Cape York Peninsula
Order Mallophaga, suborder Amblycera, family Gyropidae					
Aotiella aotophilus[11] (Ewing)	*Aotus trivirgatus*[11] (Humboldt)	Cebidae[11]	Night monkey[2]	Probably same as host[16]	Central and South America: Nicaragua to Argentina[2]
Gliricola porcelli (Schrank) (slender guinea pig louse)[14]	*Cavia aperea*[3] Erxleben	Caviidae[3]	Guinea pig	Probably worldwide	Colombia,[3] Venezuela, south to Brazil, N. Argentina
	Cavia fulgida Wagler				Brazil[15]
	Cavia porcellus (Linnaeus)				Brazil and Peru originally; now worldwide in laboratories[2]
	Cavia tschudii[3] Fitzinger	Caviidae[3]	Guinea pig[2]		Peru, Argentina, N. Chile[3]

Order Mallophaga, suborder Amblycera, family Gyropidae—*Continued*

Louse	Host			Distribution	
	Scientific name	Family	Common name	Louse	Host
Gyropus ovalis[11] Burmeister (oval guinea pig louse)[14]	*Cavia aperea* Erxleben		Cavy	Probably worldwide	Colombia, Venezuela, south to Brazil, N. Argentina
	Cavia fulgida Wagler		Cavy		Brazil[15]
	Cavia porcellus (Linnaeus)		Cavy		Brazil; Peru originally; now worldwide in laboratories[2]
	Cavia tschudii Fitzinger		Cavy		See above[3]
Macrogyropus dicotylis[11] (Macalister)	*Tayasau pecari* (Link)	Tayassuidae	White-lipped peccary	Costa Rica, Panama, Venezuela, British[16] Guiana, Brazil, Argentina; probably same as hosts	Mexico: Oaxaca, Veracruz; to Argentina, Paraguay
	Tayassu tajacu[11] (Linnaeus)		Collared peccary		U.S.: Texas, New Mexico, Arizona; south to Argentina
Pitrufquenia coypus[9] Marelli	*Myocastor coypus*[9] (Molina)	Myocastoridae	Nutria or coypu	Chile,[16] U.S.[17]	Native to South America; introduced to North America, Europe, N. Asia, E. Africa

Order Mallophaga, suborder Amblycera, family Menoponidae

Louse	Scientific name	Family	Common name	Distribution: Louse	Distribution: Host
Amyrsidea desousai[10] (Kéler)	*Numida meleagris*[18] (Linnaeus)	Numididae[18]	Helmeted guinea fowl[13]	North America, British East Africa, Zululand[18]	Most of Africa; Madagascar; introduced to North America[13]
Amyrsidea lagopi (Grube)	*Lagopus lagopus* (Linnaeus)	Phasianidae[13]	Willow ptarmigan[18]	North America	Widespread in Holarctic region
	Lagopus leucurus (Richardson)		White-tailed ptarmigan		U.S.: Alaska to N. New Mexico; introduced to California
Amyrsidea megalosoma (Overgaard)	*Bonasa umbellus* (Linnaeus)		Ruffed grouse	Probably same as hosts	Forests of Canada and continental U.S.
	Phasianus colchicus Linnaeus		Ring-necked pheasant		Palearctic region; introduced to North America, Hawaii, New Zealand, Japan, Australia
	Tympanuchus phasianellus[13] (Linnaeus)		Sharp-tailed grouse		U.S.: Alaska to New Mexico
	Tympanuchus cupido[18] (Linnaeus)		Greater prairie chicken		Canada to U.S.: North Dakota to Texas
Amyrsidea minuta Emerson	*Pavo cristatus* Linnaeus		Indian peafowl[13]	Probably worldwide with host	Sri Lanka; subcontinent of India; introduced worldwide
Amyrsidea perdicis (Denny)	*Perdix perdix* (Linnaeus)		Gray partridge[18]	Probably same as host	Widespread in Palearctic region; introduced to Canada and U.S.
Amyrsidea phaeostoma[18] (Nitzsch)	*Pavo cristatus*[18] Linnaeus	Phasianidae[13]	Indian peafowl[13]	North America,[18] Thailand[20]	Sri Lanka; subcontinent of India;[13] introduced worldwide

Louse	Host			Distribution	
	Scientific name	Family	Common name	Louse	Host

Order Mallophaga, suborder Amblycera, family Menoponidae—*Continued*

Louse	Host scientific name	Host family	Host common name	Distribution: Louse	Distribution: Host
Amyrsidea spicula Carriker	*Ortalis vetula* (Wagler)	Cracidae	Plains chachalaca	Mexico: Veracruz[21]	U.S.: S. Texas; Mexico; Central America: Belize to Nicaragua
Bonomiella columbae Emerson	*Columba livia* Gmelin	Columbidae[18]	Domestic pigeon (rock pigeon)	North America[10]	Worldwide
Ciconiphilus pectiniventris (Harrison)	*Anser albifrons* (Scopoli)	Anatidae[13]	Greater white-fronted goose	North America	Holarctic region
	Anser anser (Linnaeus)		Greylag goose		Widespread Palearctic region, India, China
	Anser caerulescens[13] (Linnaeus)		Snow goose		Russia: Siberia; Arctic America to Mexico
	Anser canagica (Sevastianov)		Emperor goose[10]		Russia: Siberia; U.S.: Alaska to California
	Anser fabalis Latham		Bean goose		Widespread Palearctic region, Iran, China, Japan
	Anser rossii Cassin		Ross's goose		Canada to S. U.S.
	Branta bernicla (Linnaeus)		Brent goose		N. Holarctic region
	Branta canadensis (Linnaeus)		Canada goose		N. North America to Mexico and Bahamas
	Branta leucopsis (Bechstein)		Barnacle goose		N. Palearctic region
Clayia theresae[10] Hopkins	*Numida meleagris* (Linnaeus)	Numididae	Helmeted guinea fowl	North America,[10] Uganda[22]	Most of Africa; Madagascar; introduced to North America
Colpocephalum tausi (Ansari)	*Meleagris gallopavo* Linnaeus	Phasianidae	Turkey	North America[10]	U.S. to S. Mexico: Fairly common locally in open woodland or forest clearings
	Numida meleagris (Linnaeus)	Numididae	Helmeted guinea fowl		Most of Africa; Madagascar; introduced to North America
	Pavo cristatus Linnaeus	Phasianidae	Indian peafowl		Sri Lanka; subcontinent of India; introduced worldwide
Colpocephalum turbinatum Denny	*Zenaida asiatica* (Linnaeus)	Columbidae	White-winged dove	South Africa:[23] Natal; North America[10]	S.W. U.S. to N. Chile
Hohorstiella lata (Piaget)	*Columba livia* Gmelin		Domestic pigeon (rock pigeon)	North America	Worldwide
Holomenopon leucoxanthum (Burmeister)	*Anas platyrhynchos* Linnaeus	Anatidae	Domestic duck (mallard)	North America	Holarctic region; introduced to other regions
	Cairina moschata (Linnaeus)		Muscovy duck		Mexico to Argentina
Menacanthus cornutus (Schrömmer)	*Gallus gallus* (Linnaeus)	Phasianidae	Chicken (red jungle fowl)	U.S.: Oklahoma, Alabama, Georgia;[24] probably worldwide[25]	Worldwide
Menacanthus numidae[10] (Giebel)	*Numida meleagris*[13] (Linnaeus)	Numididae[13]	Helmeted guinea fowl[13]	North America[10]	Most of Africa; Madagascar; introduced to North America[13]

Appendix A. Hosts and distribution of lice in the order Mallophaga—*Continued*

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host
Order Mallophaga, suborder Amblycera, family Menoponidae—*Continued*					
Menacanthus pallidulus (Neumann)	*Gallus gallus* (Linnaeus)	Phasianidae	Chicken (red jungle fowl)	Worldwide[25]	Worldwide
Menacanthus pricei[26] Wiseman	*Colinus virginianus* (Linnaeus)	Odontophoridae	Northern bobwhite quail	S.E. U.S.[26]	U.S. to Guatemala; introduced to West Indies
Menacanthus stramineus[10] (Nitzsch) (chicken body louse)[14]	*Gallus gallus* (Linnaeus)	Phasianidae	Chicken (red jungle fowl)	Worldwide[25]	Worldwide
	Meleagris gallopavo Linnaeus		Turkey		U.S. to S. Mexico: Fairly common locally in open woodland or forest clearings
	Numida meleagris (Linnaeus)	Numididae	Helmeted guinea fowl		Most of Africa; Madagascar; introduced to North America
	Pavo cristatus Linnaeus	Phasianidae	Indian peafowl		Sri Lanka; subcontinent of India; introduced worldwide
	Phasianus colchicus Linnaeus		Ring-necked pheasant		(See above)
Menopon gallinae[10] (Linnaeus) (shaft louse)[14]	*Gallus gallus* (Linnaeus)		Chicken (red jungle fowl)	Worldwide	Worldwide
	Meleagris gallopavo Linnaeus		Turkey		(See above)
	Numida meleagris (Linnaeus)	Numididae	Helmeted guinea fowl		(See above)
	Phasianus colchicus Linnaeus	Phasianidae	Ring-necked pheasant		(See above)
Menopon pallens[10] Clay	*Alectoris graeca* (Meisner)		Rock partridge	North America[10]	Alps of France, Italy to Austria, Bulgaria, Greece
	Perdix perdix (Linnaeus)		Gray partridge		Widespread in Palearctic region; introduced to Canada and U.S.
Numidicola antennatus (Kellogg & Paine)	*Numida meleagris* (Linnaeus)	Numididae	Helmeted guinea fowl	North America	(See above)
Somaphantus lusius Paine	*Numida meleagris* (Linnaeus)		Helmeted guinea fowl	North America	
Trinoton anserinum (J.C. Fabricius) (goose body louse)[14]	*Anser albifrons* (Scopoli)	Anatidae	Greater white-fronted goose	Probably same as hosts	Holarctic region
	Anser anser Linnaeus		Greylag goose		Widespread Palearctic region, India, China
	Anser caerulescens (Linnaeus)		Snow goose		Russia: Siberia; Arctic America to Mexico
	Branta canadensis (Linnaeus)		Canada goose		N. North America to Mexico and Bahamas
	Cygnus buccinator[13] Richardson	Anatidae[13]	Trumpeter swan[13]		W. North America[13]
	Cygnus colombianus (Ord)		Tundra swan		N. Eurasia

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host
Order Mallophaga, suborder Amblycera, family Menoponidae—*Continued*					
Trinoton anserinum[10] (J.C. Fabricius) (goose body louse)[14] **—*Continued***	*Cygnus cygnus* Linnaeus		Whooper swan		N., C. Palearctic region
	Cygnus olor (Gmelin)		Mute swan		N., C. Eurasia; introduced to Australia, U.S.
Trinoton querquedulae[10] (Linnaeus) (large duck louse)[14]	*Aix sponsa* (Linnaeus)		Wood duck	South Africa, North and South America,[10] Europe; probably worldwide	Canada to Mexico, West Indies
	Anas acuta Linnaeus		Northern pintail		Holarctic and Oriental regions
	Anas americana Gmelin		American wigeon		U.S., Canada
	Anas bahamensis Linnaeus		White-cheeked pintail		Widespread South America, West Indies
	Anas clypeata Linnaeus		Northern shoveler		Holarctic region
	Anas crecca Linnaeus		Common teal		Holarctic region
	Anas discors Linnaeus		Blue-winged teal		U.S.: Alaska to Arizona, Florida, Hawaii
	Anas falcata Georgi		Falcated teal		E. Asia
	Anas formosa Georgi		Baikal duck		Russia: N., C. Siberia
	Anas penelope Linnaeus		European wigeon		Palearctic and Oriental regions
	Anas platyrhynchos Linnaeus		Domestic duck (mallard)		Holarctic region; introduced to other regions
	Anas rubripes Brewster		American black duck		E. North America
	Anas strepera Linnaeus		Gadwall		Holarctic region
	Aythya affinis (Eyton)		Lesser scaup		N., C. North America
	Aythya americana (Eyton)		Redhead		N. Nearctic region
	Aythya baeri (Radde)		Baer's pochard		E. Eurasia
	Aythya ferina (Linnaeus)		Common pochard		Palearctic and Oriental regions
	Aythya fuligula (Linnaeus)		Tufted duck		Palearctic region
	Aythya marila (Linnaeus)		Greater scaup		Holarctic region
	Bucephala albeola[13] (Linnaeus)	Anatidae[13]	Bufflehead[13]		U.S. and Canada: Alaska to Mexico[13]

Order Mallophaga, suborder Amblycera, family Menoponidae—*Continued*

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host
Trinoton querquedulae[10] (Linnaeus) (large duck louse)[14] —***Continued***	*Bucephala islandica* (Gmelin)		Barrow's goldeneye		N. North America, S.W. Greenland, Iceland
	Clangula hyemalis (Linnaeus)		Long-tailed duck		Holarctic region
	Histrionicus histrionicus (Linnaeus)		Harlequin duck		Holarctic region
	Lophodytes cucullatus (Linnaeus)		Hooded merganser		U.S. and Canada: Alaska to Mexico
	Melanitta fusca (Linnaeus)		White-winged scoter		Holarctic region
	Melanitta perspicillata (Linnaeus)		Surf scoter		N. and W. North America
	Mergus merganser Linnaeus		Common merganser		Holarctic region
	Mergus serrator Linnaeus		Red-breasted merganser		Holarctic region
	Oxyura dominica Linnaeus		Masked duck		Neotropical region; U.S.: Texas
	Oxyura jamaicensis (Gmelin)		Ruddy duck		Nearctic and Neotropical regions
	Somateria fischeri (Brandt)		Spectacled eider		Russia: N. Siberia; U.S.: Alaska
	Somateria spectabilis (Linnaeus)		King eider		Holarctic region

Order Mallophaga, suborder Amblycera, family Trimenoponidae

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host
Chinchillophaga clayae[11] Emerson	*Dolichotis patagonum*[11] (Zimmermann)	Caviidae[11]	Mara[2]	England: Zoological Garden of London;[4] South America	Argentina: Patagonia[2]
Cummingsia intermedia[16] Werneck	*Marmosa dryas* Thomas	Didelphidae	Venezuelan mouse-opossum	Brazil	W. Venezuela, E. Colombia
	Marmosa incana (Lund)		Brazilian mouse-opossum		E. Brazil
Cummingsia maculata Ferris	*Lestoros inca* (Thomas)	Caenolestidae	"Rat" opossum	Peru	Andean zone of S. Peru
Cummingsia peramydis Ferris	*Monodelphis brevicaudata* (Erxleben)	Didelphidae	Short bare-tailed opossum	Brazil	E. and C. Brazil, French Guiana, Guyana, Surinam, W. Venezuela, adjacent Colombia
	Monodelphis domestica (Wagner)		Opossum		E. and C. Brazil, Bolivia, Paraguay
Harrisonia uncinata[11] Ferris	*Hoplomys gymnurus* (Thomas)	Echimyidae	Armored rat	Ecuador, Brazil,[16] Trinidad	Honduras south through Costa Rica, and Panama to Colombia and Ecuador

Louse	Host			Distribution	
	Scientific name	Family	Common name	Louse	Host

Order Mallophaga, suborder Amblycera, family Trimenoponidae—*Continued*

Harrisonia uncinata[11] Ferris	*Proechimys guyannensis*[11] (E. Geoffroy)	Echimyidae[11]	Cayenne spiny rat[2]		Colombia to the Guianas,[15] N.E. Peru, N.W. Bolivia, C. Brazil
	Proechimys semispinosus (Tomes)		Spiny rat		Honduras to Peru and Amazonian Brazil
Hoplomyophilus nativus Mendez	*Hoplomys gymnurus* (Thomas)		Armored rat	Panama, Nicaragua[16]	Honduras south through Costa Rica, and Panama to Colombia and Ecuador
	Proechimys semispinosus (Tomes)		Spiny rat		Honduras to Peru and Amazonian Brazil
Philandesia chinchillae (Werneck)	*Chinchilla lanigera* (Molina)	Chinchillidae	Chinchilla	Argentina, Peru, Bolivia	Andes mts. of Chile and Bolivia
	Lagidium peruanum Meyen		Peruvian hare		Peru
	Lagidium viscacia (Molina)		Mountain viscacha		Bolivia, Peru, Chile, W. Argentina
Philandesia mazzai (Werneck)	*Chinchilla lanigera* (Molina)		Chinchilla	Argentina: Juyjuy; Bolivia: Murillo; Peru: Occabamba Pass	Andes mts. of Chile and Bolivia
	Lagidium peruanum Meyen		Peruvian hare		Peru
	Lagidium viscacia (Molina)		Mountain viscacha		Bolivia, Peru, Chile, W. Argentina
Philandesia townsendi Kellogg & Nakayama	*Lagidium peruanum* Meyen		Peruvian hare	Peru, Bolivia	Peru
	Lagidium viscacia (Molina)		Mountain viscacha		Bolivia, Peru, Chile, W. Argentina

Order Mallophaga, suborder Ischnocera, family Philopteridae

Anaticola anseris anseris[28] (Linnaeus) (slender goose louse)[14]	*Anser anser*[13] Linnaeus	Anatidae[13]	Greylag goose[13]	North America[28]	Worldwide[13] (domestic goose); Palearctic region, India, China (wild form)
Anaticola anseris serratus[28] (Nitzsch)	*Anser albifrons* (Scopoli)		Greater white-fronted goose	Probably same as host	Holarctic region
Anaticola crassicornis (Scopoli) (slender goose louse)[14]	*Aix sponsa* (Linnaeus)		Wood duck	Probably same as hosts	Canada to Mexico, West Indies
	Anas acuta Linnaeus		Northern pintail		Holarctic and Oriental regions
	Anas clypeata Linnaeus		Northern shoveler		Holarctic region
	Anas crecca Linnaeus		Common teal		Holarctic region
	Anas penelope Linnaeus		Eurasian wigeon		Palearctic and Oriental regions

Order Mallophaga, suborder Ischnocera, family Philopteridae—*Continued*

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host
Anaticola crassicornis (Scopoli) (slender goose louse)[14] —***Continued***	*Anas platyrhynchos*[13] Linnaeus	Anatidae[13]	Domestic duck (mallard)[13]		Worldwide (domestic duck), Holarctic[13] region (wild form)
	Anas strepera Linnaeus		Gadwall		Holarctic region
	Aythya affinis (Eyton)		Lesser scaup		N., C. North America
	Aythya ferina (Linnaeus)		Common pochard		Palearctic and Oriental regions
	Bucephala islandica (Gmelin)		Barrow's goldeneye		N. North America, S.W. Greenland, Iceland
	Clangula hyemalis (Linnaeus)		Long-tailed duck		Holarctic region
	Melanitta fusca (Linnaeus)		White-winged scoter		Holarctic region
	Melanitta nigra (Linnaeus)		Black scoter		Palearctic region; Canada; U.S.: Alaska
	Melanitta perspicillata (Linnaeus)		Surf scoter		N. North America
	Mergus serrator Linnaeus		Red-breasted merganser		Holarctic region
	Somateria mollissima (Linnaeus)		Common eider		Holarctic region
	Somateria spectabilis (Linnaeus)		King eider		Holarctic region
Anatoecus icterodes[18] (Nitzsch)	*Anas clypeata* (Linnaeus)		Northern shoveler	South Africa:[29] Transvaal, Natal; Namibia: Tananzu; North America;[28] probably same as hosts	Holarctic region
	Anas crecca Linnaeus		Common teal		Holarctic region
	Anas penelope Linnaeus		Eurasian wigeon		Palearctic and Oriental regions
	Anas strepera Linnaeus		Gadwall		Holarctic region
	Anser albifrons (Scopoli)		Greater white-fronted goose		Holarctic region
	Anser anser Linnaeus		Greylag goose		Worldwide (domestic goose); Palearctic region, India, China (wild form)
	Anser caerulescens (Linnaeus)		Snow goose		Russia: Siberia; North America to Mexico
	Anser fabalis Latham		Bean goose		N., C. Eurasia
	Aythya affinis (Eyton)		Lesser scaup		N., C. North America
	Aythya americana (Eyton)		Redhead		Nearctic region

Order Mallophaga, suborder Ischnocera, family Philopteridae—*Continued*

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host
Anatoecus icterodes[18] (Nitzsch) —***Continued***	*Aythya ferina*[13] (Linnaeus)	Anatidae[13]	Common pochard[13]		Palearctic and Oriental regions[13]
	Aythya fuligula (Linnaeus)		Tufted duck		Palearctic region
	Bucephala clangula (Linnaeus)		Common goldeneye		Holarctic region
	Bucephala islandica (Gmelin)		Barrow's goldeneye		N. North America, S.W. Greenland, Iceland
	Clangula hyemalis (Linnaeus)		Long-tailed duck		Holarctic region
	Cygnus olor (Gmelin)		Mute swan		N., C. Eurasia
	Mergus merganser Linnaeus		Common merganser		Holarctic region
	Mergus serrator Linnaeus		Red-breasted merganser		Holarctic region
	Somateria mollissima (Linnaeus)		Common eider		Holarctic region
	Tadorna tadorna (Linnaeus)		Common shelduck		Palearctic and Oriental regions
Campanulotes compar[30] (Burmeister) (small pigeon louse)[14]	*Columba livia* Gmelin	Columbidae	Domestic pigeon (rock pigeon)	Worldwide[28]	Worldwide
Chelopistes meleagridis[40] (Linnaeus)	*Meleagris gallopavo* Linnaeus	Phasianidae	Turkey	North America	U.S. to S. Mexico: Fairly common locally in open woodland or forest clearings
Chelopistes texanus[28] Emerson	*Ortalis vetula* (Wagler)	Cracidae	Plains chachalaca	U.S.: Texas; Mexico;[31] Central America	Neotropical region
Colinicola docophoroides (Piaget)	*Callipepla californica* (Shaw)	Odontophoridae	California quail	Probably same as host[28]	W. North America
Colinicola mearnsi Emerson	*Cyrtonyx montezumae* (Vigors)		Montezuma quail	North America	S.W. U.S. to S. Mexico
Colinicola numidiana (Denny)	*Colinus virginianus* (Linnaeus)		Northern bobwhite quail	North America	U.S. to Guatemala
Colinicola pallida Emerson	*Callipepla squamata* (Vigors)		Scaled quail	North America	S. U.S. to Central America
Columbicola columbae[30] (Linnaeus) (slender pigeon louse)[14]	*Columba livia* Gmelin	Columbidae	Domestic pigeon (rock pigeon)	Worldwide[30]	Worldwide
Cuclotogaster heterogrammicus[28] (Nitzsch)	*Perdix perdix* (Linnaeus)	Phasianidae	Gray partridge	Probably same as host[28]	Palearctic region; introduced to Canada and U.S.

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host
Order Mallophaga, suborder Ischnocera, family Philopteridae—*Continued*					
Cuclotogaster heterographus[25] (Nitzsch) (chicken head louse)[14]	*Gallus gallus*[13] (Linnaeus)	Phasianidae[13]	Chicken (red jungle fowl)[13]	Worldwide[25]	Worldwide[13]
	Phasianus colchicus Linnaeus		Ring-necked pheasant[18]		Palearctic region; introduced to North America, Hawaii, New Zealand, Japan, Australia
Cuclotogaster obscurior[28] Hopkins	*Alectoris graeca chukar* (Meisner)		Chukar	North America;[28] probably same as host	Alps of France, Italy to Austria, Bulgaria; introduced to North America
Goniocotes chrysocephalus Giebel	*Phasianus colchicus* Linnaeus		Ring-necked pheasant	Probably same as host	(See above)
Goniocotes gallinae[25] (de Geer) (fluff louse)[14]	*Gallus gallus* (Linnaeus)		Chicken (red jungle fowl)[13]	Worldwide[25]	Worldwide
Goniocotes maculatus[27] Taschenberg	*Numida meleagris* (Linnaeus)	Numididae	Helmeted guinea fowl	Probably same as host	Most of Africa; Madagascar; introduced to North America
Goniocotes microthorax[28] (Stephens)	*Alectoris graeca* (Meisner)	Phasianidae	Rock partridge		Alps of France, Italy to Austria, Bulgaria, Greece
	Perdix perdix (Linnaeus)		Gray partridge		Widespread Palearctic region; introduced to Canada and U.S.
Goniocotes parviceps (Piaget)	*Pavo cristatus* Linnaeus		Indian peafowl	North America,[28] Thailand[20]	Sri Lanka; subcontinent of India; introduced worldwide
Goniocotes rectangulatus Nitzsch	*Pavo cristatus* Linnaeus		Indian peafowl	Probably same as host[28]	(See above)
Goniodes bonasus Emerson	*Bonasa umbellus* (Linnaeus)		Ruffed grouse	U.S.: Colorado, Montana, New York	Forests of Canada, Alaska, and other U.S states
Goniodes centrocerci Simon	*Centrocercus urophasianus* (Bonaparte)		Sage grouse	U.S.: Nebraska,[32] Wyoming, Idaho, Montana, Oregon	W. North America
Goniodes colchici Denny	*Phasianus colchicus* Linnaeus		Ring-necked pheasant	Great Britain, Afghanistan,[33] North America[28]	(See above)
Goniodes corpulentus Kellogg & Mann	*Dendragapus canadensis* (Linnaeus)		Spruce grouse	U.S.: Alaska, Montana; Canada: Manitoba, Ontario[32]	N. North America; U.S.: Oregon to New Hampshire
Goniodes cupido Rudow	*Tympanuchus cupido* (Linnaeus)		Greater prairie chicken	Canada to U.S.: Texas, Nebraska, Oklahoma	Canada to C. U.S. to Texas
	Tympanuchus pallidicinctus (Ridgway)		Lesser prairie chicken		S.W. U.S.
Goniodes dispar Burmeister	*Alectoris graeca chukar* (Meisner)		Chukar	British Isles; Hungary; Russia: Estonia; Poland; India: Ladakh; Arabia; Afghanistan;[33] U.S.: California, Montana, Ohio, Virginia, Washington; Canada: British Columbia, Saskatchewan[32]	Alps of France, Italy to Austria, Bulgaria; introduced to North America

Louse	Host			Distribution	
	Scientific name	Family	Common name	Louse	Host
Order Mallophaga, suborder Ischnocera, family Philopteridae—*Continued*					
Goniodes dispar Burmeister —***Continued***	*Perdix perdix*[13] (Linnaeus)		Gray partridge[13]		Widespread Palearctic region; introduced to Canada and U.S.[13]
Goniodes dissimilis[25] (Denny) (brown chicken louse)[14]	*Gallus gallus* (Linnaeus)	Phasianidae[13]	Chicken (red jungle fowl)	Worldwide[33]	Worldwide
Goniodes gigas[28] (Taschenberg) (large chicken louse)[14]	*Gallus gallus* (Linnaeus)			Worldwide	Worldwide
	Numida meleagris (Linnaeus)	Numididae	Helmeted guinea fowl		Most of Africa; Madagascar; introduced to North America
Goniodes lagopi[28] (Linnaeus)	*Lagopus lagopus* (Linnaeus)	Phasianidae	Willow ptarmigan	U.S.: Alaska;[32] Canada; N.E. Greenland; Iceland; Scotland; Estonia[33]	N. Holarctic region
	Lagopus mutus (Montin)		Rock ptarmigan	Probably same as host	N. Holarctic region
Goniodes leucurus[32] Emerson	*Lagopus leucurus* (Richardson)		White-tailed ptarmigan	Alaska: Talkeetna mts.[32]	N. Nearctic region
Goniodes meinertzhageni[28] Clay	*Pavo cristatus* Linnaeus		Indian peafowl	India: Delhi[33]	Sri Lanka; subcontinent of India; introduced worldwide
Goniodes merriamanus[32] Packard	*Dendragapus obscurus* (Say)		Blue grouse	U.S.: Idaho, Wyoming, Montana[32]	N.W. North America
Goniodes nebraskensis Carriker	*Tympanuchus phasianellus* (Linnaeus)		Sharp-tailed grouse	Canada: Manitoba; U.S.: Montana, North Dakota, Nebraska	W. North America
Goniodes numidae Mjöberg (guinea feather louse)[14]	*Numida meleagris* (Linnaeus)	Numididae	Helmeted guinea fowl	South Africa: Transvaal, Namibia;[23] introduced to U.S.[32]	Most of Africa; Madagascar; introduced to North America
Goniodes ortygis[28] Denny	*Colinus virginianus* (Linnaeus)	Odontophoridae	Northern bobwhite quail	U.S.: Washington, Texas, Florida[28]	U.S. to Guatemala
Goniodes pavonis (Linnaeus)	*Pavo cristatus* Linnaeus	Phasianidae	Indian peafowl	Thailand,[20] India, Vietnam,[33] South Africa[22]	Sri Lanka; subcontinent of India; introduced worldwide
Goniodes pictus Emerson	*Oreortyx pictus* (Douglas)	Odontophoridae	Mountain quail	U.S.: California[28]	W. North America
Goniodes squamatus Emerson	*Callipepla squamata* (Vigors)		Scaled quail	U.S.: New Mexico, Texas	S. U.S. to Central America
Goniodes stefani Clay & Hopkins	*Callipepla californica* (Shaw)		California quail	U.S.: California; Canada: British Columbia	W. North America
Goniodes submamillatus Emerson	*Callipepla gambelii* Gambel		Gambel's quail	U.S.: Arizona[32]	S.W. U.S. to W. Mexico
Lagopoecus affinis (Children)	*Lagopus lagopus* (Linnaeus)	Phasianidae	Willow ptarmigan	Probably same as host	N. Holarctic region

Order Mallophaga, suborder Ischnocera, family Philopteridae—*Continued*

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host
Lagopoecus affinis (Children) —***Continued***	*Lagopus leucurus*[13] (Richardson)		White-tailed ptarmigan[13]		N. Nearctic region[13]
	Lagopus mutus (Montin)		Rock ptarmigan		N. Holarctic region
Lagopoecus californicus[28] (Kellogg & Chapman)	*Oreortyx pictus* (Douglas)	Odontophoridae[13]	Mountain quail	U.S.: California, Nevada[32]	W. North America
Lagopoecus colchicus Emerson	*Phasianus colchicus* Linnaeus	Phasianidae	Ring-necked pheasant[18]	U.S.: Utah, Illinois, Montana, Michigan	(See above)
Lagopoecus gambelii Emerson	*Callipepla gambelii* Gambel	Odontophoridae	Gambel's quail[13]	U.S.: Arizona	S.W. U.S. to W. Mexico
Lagopoecus gibsoni Hopkins	*Centrocercus urophasianus* (Bonaparte)	Phasianidae	Sage grouse	U.S.: Montana, Idaho, Oregon, Wyoming	W. North America
Lagopoecus obscurus Emerson	*Dendragapus obscurus* (Say)		Blue grouse	Canada: British Columbia; U.S.: Washington, Montana, California	N.W. North America
Lagopoecus perplexus (Kellogg & Chapman)	*Tympanuchus phasianellus* (Linnaeus)		Sharp-tailed grouse	Canada: Ontario; U.S.: Washington, Montana, California	W. North America
Lagopoecus sinensis (Sugimoto)	*Gallus gallus* (Linnaeus)		Chicken (red jungle fowl)	China,[36] North America[28]	Worldwide
Lagopoecus umbellus Emerson	*Bonasa umbellus* (Linnaeus)		Ruffed grouse	Canada: Ontario;[32] U.S.: New York, Pennsylvania, Idaho[28]	Forests of Canada, Alaska, and other U.S states
Lipeurus caponis[25] (Linnaeus) (wing louse)[14]	*Gallus gallus* (Linnaeus)		Chicken (red jungle fowl)	Worldwide[25]	Worldwide
Lipeurus lawrensis[23] *lawrensis* Bedford	*Numida meleagris* (Linnaeus)	Numididae	Helmeted guinea fowl	Namibia[29]	Most of Africa; Madagascar; introduced to North America
Lipeurus lawrensis[35] *tropicalis* Peters	*Acryllium vulturinum* (Hardwicke)		Vulturine guinea fowl	Tropical and subtropical regions:[32] Brazil, Venezuela, Panama Canal Zone, British West Indies, Puerto Rico, Cuba, Liberia, Ethiopia, India[28]	N.E. Africa
	Agelastes meleagrides Bonaparte		White-breasted guinea fowl		Liberia to Ghana
	Gallus gallus (Linnaeus)	Phasianidae	Chicken (red jungle fowl)		Worldwide
	Guttera plumifera (Cassin)	Numididae	Plumed guinea fowl		W.C. Africa
	Agelastes niger (Cassin)		Black guinea fowl		W.C. Africa
Lipeurus maculosus[28] Clay	*Phasianus colchicus* Linnaeus	Phasianidae	Ring-necked pheasant	Scotland, Hungary, Vietnam,[37] Canada, U.S.;[32] probably same as host	(See above)

Louse	Host			Distribution	
	Scientific name	Family	Common name	Louse	Host
Order Mallophaga, suborder Ischnocera, family Philopteridae—*Continued*					
Lipeurus numidae[37] (Denny) (slender guinea louse)[14]	*Numida meleagris*[13] (Linnaeus)	Numididae[13]	Helmeted guinea fowl[13]	Subsaharan Africa[37]	Most of Africa; Madagascar;[13] introduced to North America
Lipeurus pavo[37] Clay	*Pavo cristatus* Linnaeus	Phasianidae	Indian peafowl	India;[32, 37] introduced to other countries with host	Sri Lanka; subcontinent of India; introduced worldwide
Ornithobius bucephalus[38] *bucephalus* (Giebel)	*Cygnus olor* (Gmelin)	Anatidae	Mute swan	England: Zoological garden of London; Argentina: Patagonia[38]	N., C. Eurasia
Ornithobius cygni (Linnaeus)	*Cygnus cygnus* Linnaeus		Whooper swan	Scotland; Ireland; probably same as host	Palearctic region
Ornithobius goniopleurus Denny	*Branta canadensis* (Linnaeus)		Canada goose	Probably same as host	Nearctic region
Ornithobius hexophthalmus (Nitzsch)	*Branta leucopsis* (Bechstein)		Barnacle goose	Probably same as host	Palearctic region
Ornithobius mathisi (Neumann)	*Anser albifrons* (Scopoli)		Greater white-fronted goose	Probably same as host	Holarctic region
	Anser anser Linnaeus		Greylag goose	Probably same as host	Widespread Palearctic region, India, China
Ornithobius waterstoni reconditus Timmermann	*Olor colombianus* (Ord)		Whistling swan	U.S.: Wisconsin, Wyoming	N. Holarctic region
Ornithobius waterstoni waterstoni Timmermann	*Olor buccinator* Richardson		Trumpeter swan	England: Zoological garden of London;[38] North America[23]	W. North America
Oxylipeurus callipeplus[32] (Carriker)	*Callipepla squamata* (Vigors)	Odontophoridae	Scaled quail	U.S.: Texas[32]	S. U.S. to Central America
Oxylipeurus clavatus (McGregor)	*Colinus virginianus* (Linnaeus)		Northern bobwhite quail	U.S.: Maryland, Oklahoma	U.S. to Guatemala
Oxylipeurus corpulentus[40] Clay	*Meleagris gallopavo* Linnaeus	Phasianidae	Turkey	S.E. U.S.[40]	U.S. to S. Mexico: Fairly common locally in open woodland or forest clearings
Oxylipeurus ellipticus[32] (Kéler)	*Callipepla californica* (Shaw)	Odontophoridae	California quail	U.S.: Arizona[41]	W. North America
	Callipepla gambelii Gambel		Gambel's quail		S.W. U.S. to W. Mexico
Oxylipeurus montezumae Emerson	*Cyrtonyx montezumae* (Vigors)		Montezuma quail	U.S.: Arizona[32]	S.W. U.S. to S. Mexico
Oxylipeurus polytrapezius[40] (Burmeister) (slender turkey louse)[14]	*Meleagris gallopavo* Linnaeus	Phasianidae	Turkey	Probably worldwide[40]	U.S. to S. Mexico: Fairly common locally in open woodland or forest clearings

Louse	Host			Distribution	
	Scientific name	Family	Common name	Louse	Host

Order Mallophaga, suborder Ischnocera, family Philopteridae—*Continued*

Louse	Scientific name	Family	Common name	Distribution: Louse	Distribution: Host
Physconelloides zenaidurae[28] (McGregor)	*Columba livia*[13] Gmelin	Columbidae[13]	Domestic pigeon[13] (rock pigeon)	North America[30]	Worldwide[13]
	Zenaidura macroura (Linnaeus)		Mourning dove		S. Canada to Panama; West Indies
Struthiolipeurus rheae[39] Harrison	*Rhea americana* (Linnaeus)	Rheidae	Greater rhea	Argentina; introduced to U.S.,[39] zoological gardens	Bolivia, Paraguay, S.E. Brazil, Uruguay, south to S.C. Argentina: Rio Negro

Order Mallophaga, suborder Ischnocera, family Trichodectidae

Louse	Scientific name	Family	Common name	Distribution: Louse	Distribution: Host
Bovicola adenota[11] Bedford	*Kobus kob*[11] (Erxleben)	Bovidae[11]	Buffon's kob[42]	Uganda: Kasinga,[43] Lango District	Senegal to W. Ethiopia and Sudan;[3] N. Zaire to W. Kenya; N.W. Tanzania
	Kobus vardonii (Livingstone)		Puku		Congo, Angola,[47] Tanzania, Zambia, Zimbabwe
Bovicola alpinus Kéler	*Rupicapra rupicapra* (Linnaeus)		Chamois	Germany: Berlin, Bavaria (in captivity)	Mts.[3] of Europe and Asia Minor
Bovicola aspilopyga Werneck	*Equus burchellii boehmi* Matschie	Equidae	Grant's zebra[2]	Uganda, Tanzania[44]	S. Sudan,[47] Ethiopia, Somalia to S. Tanzania
Bovicola bovis (Linnaeus) (cattle biting louse)[14]	*Bos taurus* Linnaeus	Bovidae	European cattle	Worldwide[43]	Worldwide[2]
Bovicola breviceps[11] (Rudow)	*Lama glama* (Linnaeus)	Camelidae	Llama	Peru; Argentia: Jujuy; Zoological Garden of Washington, DC	Llama and alpaca exist[3] only as domesticated animals mainly in Peru and Bolivia; guanaco survives in the wild in same region.
	Lama guanicoe[3] (Müller)		Guanaco		
	Lama pacos[11] (Linnaeus)		Alpaca		
Bovicola caprae (Gurlt) (goat biting louse)[14]	*Capra hircus* Linnaeus	Bovidae	Goat	Most of U.S., France, Uganda, South Africa; probably worldwide	Worldwide
Bovicola concavifrons[45] (Hopkins)	*Cervus canadensis* Erxleben	Cervidae	Wapiti or American elk	Canada: Alberta (Banff)[45]	W. U.S., W. Canada
Bovicola crassipes[11] (Rudow) (Angora goat biting louse)[14]	*Capra hircus* Linnaeus	Bovidae[3]	Goat (Angora)	U.S.: Wherever Angora goats are raised	S.E. Europe[48] through Asia Minor to Iran and Pakistan; introduced to U.S. and South Africa
Bovicola dimorpha[43] Bedford	*Nemorhedus goral*[3] (Hardwicke)		Goral	China: Hangchow[43]	N. Pakistan; India: Sikkim; Nepal; Bhutan[3]
Bovicola equi[11] (Denny) (horse biting louse)[14]	*Equus caballus* Linnaeus	Equidae	Domestic horse	Probably same as host[51]	Worldwide

Appendix A. Hosts and distribution of lice in the order Mallophaga—*Continued*

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host
Order Mallophaga, suborder Ischnocera, family Trichodectidae—*Continued*					
Bovicola equi (Denny) —***Continued***	*Equus hemionus*[3] Pallas		Asiatic wild ass[42]		Central Asia: Mongolia, north to[3] Transbaikalia (USSR), possibly to Manchuria (China)
Bovicola fulva[11] Emerson & Price	*Ammotragus lervia* (Pallas)	Bovidae[11]	Aoudad	U.S.: Texas, New Mexico[49]	N. Egypt to Morocco; Niger to Sudan; Israel; introduced to U.S.: New Mexico, Texas
Bovicola hemitragi (Cummings)	*Hemitragus jemlahicus*[11] (Hamilton-Smith)		Himalayan tahr	England: Zoological Garden of London;[43] New Zealand: South Island; Nepal	India and Pakistan: Pir Panjal Mts.,[2] Kashmir, Punjab, Kumaon; Nepal to Tibet; introduced to New Zealand[3]
Bovicola hilli Bedford	*Kobus ellipsiprymnus defassa* (Rüppell)		Defassa waterbuck	Uganda; South Africa: Natal, Zululand	Senegal to Somalia to N. South Africa[3] to Angola
	Kobus ellipsiprymnus ellipsiprymnus (Ogilby)		Common waterbuck[40]		
Bovicola jellisoni Emerson	*Ovis canadensis* Shaw		Bighorn sheep	U.S.: Alaska,[50] Montana; Canada: Alberta; Mexico: Sonora, Baja California	W. Canada, U.S., N.W. Mexico
	Ovis dalli Nelson		Dall's sheep[2]		U.S.: Alaska; to W. Canada
Bovicola limbatus (Gervais)	*Capra hircus* Linnaeus		Goat	Worldwide[51]	Worldwide
Bovicola longicornis (Nitzsch)	*Cervus canadensis* (Erxleben)	Cervidae	American elk or wapiti	Netherlands:[43] Amsterdam; Germany; North America (probably same as host)	W. U.S. and Canada
	Cervus elaphus Linnaeus		Red deer[42]		Forests of Europe and Asia[42]
Bovicola multispinosa Emerson & Price	*Pseudois nayaur* (Hodgson)	Bovidae	Blue sheep or bharal	Nepal: 20 mi N of Dhorpatan[49]	Highlands of C. Asia[2] from India to mts. of W. China
Bovicola neglectus Kéler	*Ammotragus lervia* (Pallas)		Aoudad	England: Zoological Garden of London;[43] Sudan: Khartoum; France: Zoological Garden of Vincennes; U.S.: Texas, New Mexico[49]	(See above)
Bovicola ocellata (Piaget)	*Equus asini* Linnaeus	Equidae	Domestic donkey	Uganda, Tanzania[17, 44]	Worldwide
	Equus burchellii[3] (Gray)		Burchell's zebra		*E. quagga* now extinct; other forms in Africa: Blue Nile to Orange River
Bovicola oreamnidis (Hopkins)	*Oreamnos americanus* (Blainville)	Bovidae	Rocky Mountain goat (antelope goat)	Canada: Alberta[45]	U.S.: Alaska (Cook Inlet); Canada: E. Yukon border of British Columbia, Alberta; south to U.S.: W. Montana, C. Idaho, N. Oregon
Bovicola orientalis[52] Emerson & Price	*Naemorhedus crispus* (Temminck)		Formosan serow[52]	Taiwan[52]	Taiwan[3]

Order Mallophaga, suborder Ischnocera, family Trichodectidae—*Continued*

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host
Bovicola ovis[11] (Schrank) (sheep biting louse)[14]	*Ovis aries*[11] Linnaeus	Bovidae[11]	Domestic sheep[2]	Worldwide[51]	Worldwide[3]
	Ovis canadensis[45] Shaw		Bighorn sheep		W. Canada, U.S., N.W. Mexico
Bovicola pelea[11] Bedford	*Pelea capreolus*[11] (Bechstein)		Rhebok	South Africa: Cape Province[43]	South Africa south of Zambezi River
Bovicola sedecimdecembrii Eichler	*Bison bison* (Linnaeus)		American bison	Canada: Alberta;[45] Poland[43]	Formerly N.W. and C. Canada; south through U.S.; to Mexico: Chihuahua, Coahuila
	Bison bonasus (Linnaeus)		European wisent or European bison		Formerly most of Europe
Bovicola tarandi (Mjöberg)	*Rangifer tarandus* (Linnaeus)	Cervidae	Reindeer (caribou)	Lapland, Greenland,[43] North America[28]	Arctic regions of world
Bovicola thompsoni Bedford	*Capricornis sumatrensis* (Bechstein)	Bovidae	Serow	Indonesia: Barisan,[43] Buki (Bubit), Sumatra	Southeast Asia, China, Kashmir, N. India
Bovicola tibialis[53] (Piaget)	*Dama dama*[3] (Linnaeus)	Cervidae[3]	Fallow deer	England: British Museum; Russia: Siberia; West Germany: Hamburg Zoological Museum; U.S.: California[53]	Orginally Mediterranean region of S. Europe and Asia Minor; introduced to most parts of Europe and a few areas of U.S., Australia
	Odocoileus hemionus[53] (Rafinesque)		Mule deer		W. Canada and W. U.S. south into N. Mexico
Bovicola zebrae[11] (Moreby)	*Equus zebra hartmannae*[11] Matschie	Equidae[11]	Mountain zebra	Namibia[44]	W. Namibia north into W. Angola[42] in mtn. ranges
Bovicola zuluensis Werneck	*Equus burchellii*[3] (Gray)		Burchell's zebra	South Africa: Zululand[43]	Blue Nile to Orange River,[3] S.W Somalia, S.W. Ethiopia, to South Africa, S.E. Zaire, E. Angola
Cebidicola armatus (Neumann)	*Alouatta ursina*[11] (Humboldt)	Cebidae	Ring-tailed monkey	Brazil	N. South America
	Brachyteles arachnoides (E. Geoffroy)		Woolly spider monkey		S.E. Brazil from Bahia to São Paulo[2]
Cebidicola extrarius Werneck	*Alouatta seniculus* (Linnaeus)		Red howler	Brazil	N. South America
Cebidicola semiarmatus (Neumann)	*Alouatta belzebul* (Linnaeus)		Rufous-handed howler	Brazil	N. Brazil[3]
	Alouatta caraya (Humboldt)		Black howler		N. Argentina to Brazil: Mato Grosso
	Alouatta guariba (Humboldt)		Brown howler		N. Bolivia, E. Brazil
	Alouatta ursina (Humboldt)		Ring-tailed monkey		N. South America

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host
Order Mallophaga, suborder Ischnocera, family Trichodectidae—*Continued*					
Damalinia appendiculata (Piaget)[11]	*Gazella subgutturosa* Guldenstadt[11]	Bovidae[11]	Persian gazelle[42]	Netherlands:[43] Zoological Garden of Rotterdam; England: Zoological Garden of London	Iraq to Mongolia[48]
Damalinia baxi Hopkins	*Damaliscus lunatus* (Burchell)[3]		Topi (sassaby)	Tanzania	Angola,[3] Zimbabwe, Tanzania
Damalinia chorleyi (Hopkins)	*Alcelaphus buselaphus* (Pallas)		Red hartebeest	Uganda	Senegal to W. Somalia; N. South Africa; S. Angola
Damalinia crenelata (Piaget)	*Damaliscus pygargus* (Pallas)		Bontebok	South Africa: Transvaal	South Africa: Cape Province (now only in captivity)
Damalinia forficula forficula (Piaget)	*Axis (Cervus) axis* (Erxleben)	Cervidae	Axis deer	Netherlands: Zoological Garden of Rotterdam; India	Sri Lanka, north to India:[2] Sikkim;[3] Nepal
	Axis (Cervus) porcinus (Zimmermann)		Hog deer		India, Cambodia, Vietnam,[2] Thailand; introduced to Sri Lanka
Damalinia forficula siamensis Werneck	*Muntiacus muntjak* (Zimmermann)		Muntjak[2]	Probably same as host	Manchuria in China through Korea and Siberia to W. Mongolia
Damalinia harrisoni (Cummings)	*Connochaetes gnou* (Zimmermann)	Bovidae	Black wildebeest	England: Zoological Garden of London; South Africa	South Africa, only in captivity[3]
Damalinia hendrickxi Hopkins	*Cephalophus nigrifrons* Gray		Black-fronted duiker[42]	Congo, Uganda	C. Africa[2]
Damalinia hopkinsi Bedford	*Taurotragus oryx* (Pallas)		Eland	Uganda	E. Africa to S. Africa
Damalinia maai Emerson & Price	*Cervus nippon* Temminck[11]	Cervidae	Formosan sika deer[54]	Taiwan[54]	Taiwan[54]
Damalinia martinaglia (Bedford)	*Kobus leche* Gray	Bovidae	Lechwe antelope[42]	South Africa: Zoological Garden of Johannesburg; Zambia[43]	Botswana[47] to Zambia, Congo
Damalinia meyeri (Taschenberg)	*Capreolus capreolus* (Linnaeus)	Cervidae	Roe deer	Probably same as host	Eurasia except extreme north and India[2]
Damalinia natalensis Emerson	*Tragelaphus scriptus* (Pallas)[3]	Bovidae	Bushbuck	South Africa: Natal[55]	Subsaharan Africa
Damalinia neotheileri Emerson & Price	*Connochaetes taurinus* (Burchell)[11]		White-bearded gnu[2]	Kenya; Tanzania;[56] South Africa: N. Transvaal	Much of S. Africa
Damalinia ornata Werneck	*Alcelaphus buselaphus caama* (G. Cuvier)		Cape hartebeest[42]	Botswana[43]	Now extinct[42]
Damalinia semitheileri Emerson & Price	*Connochaetes taurinus* (Burchell)		White-bearded gnu[2]	Zambia[56]	Much of S. Africa
Damalinia theileri Bedford	*Connochaetes taurinus* (Burchell)		White-bearded gnu	South Africa: N. Transvaal[43]	(See above)

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host
Order Mallophaga, suborder Ischnocera, family Trichodectidae—*Continued*					
Damalinia traguli[11] Werneck	*Tragulus javanicus*[11] (Osbeck)	Tragulidae[11]	Lesser Malayan chevrotain[2] (mouse deer)	Indonesia: Borneo, Sumatra[43]	Indonesia: Sumatra, Borneo, Java[3]
	Tragulus napu (F. Cuvier)		Larger Malayan chevrotain		Thailand: Malaysia; Indonesia: Sumatra, Borneo; Philippines: Balabac Island
Dasonyx[d] (16 spp.)	Spp. in order Hyracoidea	Procaviidae	Hyraxes (tree and rock dassies)		Africa, Near East
Eurytrichodectes[d] (2 spp.)					Africa
Eutrichophilus cercolabes[11] Mjöberg	*Coendou prehensilis*[11] (Linnaeus)	Erethizontidae	Prehensile-tailed porcupine[15]	Brazil	E. Venezuela, Guyana, C. and E. Brazil, Bolivia, Trinidad
	Sphiggurus spinosus[3] (Cuvier)		South American porcupine		Brazil, Paraguay, N. Argentina, W. Uruguay
Eutrichophilus comitans Werneck	*Sphiggurus vestitus* (Thomas)		Colombian porcupine	Venezuela, Colombia	Colombia, Venezuela
Eutrichophilus cordiceps Mjöberg	*Coendou prehensilis*[11] (Linnaeus)		Prehensile-tailed porcupine	Brazil, Paraguay	(See above)
	Sphiggurus spinosus[3] (Cuvier)		South American porcupine		(See above)
Eutrichophilus exiguus Werneck	*Coendou melanurus*[11] (Wagner)		Brazilian porcupine[48]	Guyana: Kartabo	Brazil, Guyana[48]
Eutrichophilus guyannensis Werneck	*Coendou melanurus* (Wagner)		Brazilian porcupine	Guyana: Kartabo	(See above)[3]
Eutrichophilus lobatus Ewing	*Sphiggurus vestitus*[3] (Thomas)		Colombian porcupine[15]	Venezuela, Colombia[61]	(See above)
Eutrichophilus maximus Bedford	*Coendou rothschildi*[11] Thomas		Rothschild's porcupine[42]	Panama Canal Zone: Gamboa[43]	Panama[15]
Eutrichophilus mexicanus (Rudow)	*Sphiggurus mexicanus*[3] (Kerr)		Mexican porcupine	Mexico, Guatemala	Mexico: San Luis Potosi,[3] Yucatán to W. Panama
Eutrichophilus minor Mjöberg	*Coendou prehensilis*[11] (Linnaeus)		Prehensile-tailed porcupine[15]	Brazil, Paraguay	(See above)
	Sphiggurus spinosus[3] (Cuvier)		South American porcupine		(See above)
Eutrichophilus moojeni Werneck	*Chaetomys subspinosus*[11] (Kuhl)		Thin-spined porcupine	Brazil: Espirito Santo	E., N. Brazil[42]
Eutrichophilus setosus (Giebel)	*Erethizon dorsatum* (Linnaeus)		North American porcupine	Canada, U.S.	North America
Felicola acutirostris (Stobbe)	*Atilax paludinosus* (G. Cuvier)	Herpestidae[3]	Marsh mongoose	Tanzania: Pemba,[16] Kilassa; Uganda: Kigezi	Africa[3]

[d]Validity of spp. and subspp. assigned to these two genera and to *Procavicola* and *Procaviphilus* is uncertain and awaits clarification.[11]

Louse	Host			Distribution	
	Scientific name	Family	Common name	Louse	Host

Order Mallophaga, suborder Ischnocera, family Trichodectidae—*Continued*

Louse	Scientific name	Family	Common name	Distribution: Louse	Distribution: Host
Felicola americanus[58] Emerson & Price	*Lynx rufus*[58] (Schreber)	Felidae[58]	Bobcat[58]	U.S.: Texas, Montana[58]	North America[3]
Felicola bedfordi[11] Hopkins	*Bdeogale crassicauda*[11] Peters	Herpestidae[3]	Black-tailed mongoose[42]	Kenya, Malawi[16]	E. Africa
	Bdeogale jacksoni (Thomas)		A mongoose		Kenya, Uganda
	Bdeogale nigripes Pucheran		Black-footed four-toed mongoose		Nigeria to N. Angola
Felicola braziliensis[58] Emerson & Price	*Felis colocolo*[58] Molina	Felidae[58]	Pampas cat[58]	Brazil[58]	South America
Felicola caffra[11] (Bedford)	*Felis lybica*[11] Forster (= *F. silvestris*[3] Schreber)		African wildcat[2]	South Africa: Transvaal[16]	Africa across Asia Minor[2] into S. Asia
Felicola calogaleus (Bedford)	*Herpestes pulverulentus*[11] Wagner	Herpestidae[3]	Cape grey mongoose	South Africa: Transvaal, Cape Province; Kenya; Uganda	S. Angola, Namibia,[3] South Africa
	Herpestes sanguineus (Rüppell)		Slender mongoose		Subsaharan Africa
Felicola cynictis (Bedford)	*Cynictis penicillata* (G. Cuvier)		Yellow mongoose[42]	South Africa: Transvaal, Orange Free State, Natal	S. Africa[42]
Felicola felis[58] (Werneck)	*Felis pardalis*[58] Linnaeus	Felidae[58]	Ocelot[58]	Guatemala[58]	E. South America to U.S.: Texas
Felicola genettae[11] (Fresca)	*Genetta genetta*[3] (Linnaeus)	Viverridae[11]	Small-spotted genet[42]	Spain: Vigo[16]	N.W. Africa, S. Europe
Felicola hercynianus Kéler	*Felis silvestris* Schreber	Felidae[58]	European wildcat[3] (= ancestral housecat)	Probably same as host	Europe, W. Asia; housecat worldwide[3]
Felicola inaequalis (Piaget)	*Herpestes ichneumon* (Linnaeus)	Herpestidae[3]	Egyptian mongoose[42]	Netherlands: Zoological Garden of Rotterdam; Congo; Uganda; Tanzania	Africa; S. Europe, Mediterranean countries to S. Turkey
Felicola intermedius hyaenae Hopkins	*Hyaena brunnea*[11] Thunberg	Hyaenidae	Brown hyena	Botswana[45]	Africa south of Zambezi River
Felicola intermedius intermedius (Bedford)	*Proteles cristatus*[3] (Sparrman)	Protelidae[11]	Aardwolf[2]	South Africa: Natal[16]	S. and E. Africa, Sudan, Ethiopia, Somalia, Central African Republic
Felicola juccii (Conci)	*Paguma larvata* (Hamilton-Smith)	Viverridae	Masked palm civet[42]	Burma; China: Szechwan	S. Asia; Indonesia: Sumatra, Borneo
Felicola liberiae[59] Emerson & Price	*Liberiictis kuhni* Hayman	Herpestidae[3]	Kuhn's kusimanse	Liberia: Grand Gedeh County[59]	Liberia
Felicola macrurus[11] Werneck	*Atilax paludinosus* (G. Cuvier)		Marsh mongoose	Tanzania: Mt. Kilimanjaro;[16] Congo	Africa
Felicola minimus Werneck	*Atilax paludinosus* (G. Cuvier)			Uganda, Tanzania, Congo	(See above)

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host
Order Mallophaga, suborder Ischnocera, family Trichodectidae—*Continued*					
Felicola neofelis[58] Emerson & Price	*Felis geoffroyi*[58] d'Orbigny & Gervais	Felidae[3]	Geoffroy's cat[42]	Brazil:[58] Russas, Ceará	E. South America[3]
Felicola pygidialis[11] Werneck	*Atilax paludinosus*[11] (G. Cuvier)	Herpestidae	Marsh mongoose	Uganda: Kampala;[16] Congo	Africa
Felicola rahmi Emerson & Stojanovich	*Atilax paludinosus* (G. Cuvier)		Marsh mongoose	Zaire: Kinshasa	Africa
Felicola robertsi Hopkins	*Rhynchogale melleri* (Gray)		Meller's mongoose[48]	Swaziland	S. Africa
Felicola rohani Werneck	*Herpestes auropunctatus* (Hodgson)		Small Indian mongoose	Mauritius[61]	S. Asia
	Herpestes edwardsi (E. Geoffroy)		Indian grey mongoose		E.C. Arabia to Nepal, India, Sri Lanka
	Herpestes javanicus[3] (E. Geoffroy)		Javan mongoose		S. Asia; Indonesia: Java
	Herpestes urva (Hodgson)		Crab-eating mongoose		S.E. Asia, Taiwan
Felicola setosus Bedford	*Paracynictis selousi* (De Winton)		Selous' meerkat[42]	South Africa:[16] Transvaal, Zululand	S. Africa
Felicola siamensis Emerson	*Felis bengalensis* Kerr	Felidae	Leopard cat	Malaysia: Negeri Sembilan[57]	S. Asia, Borneo, Philippines
Felicola similis[58] Emerson & Price	*Felis yagouaroundi*[58] E. Geoffroy		Jaguarundi[58]	Brazil; Paraguay;[58] Venezuela; U.S.: Arizona	Mexico to Patagonia; U.S.: occasionally in Texas, Arizona
Felicola spenceri[11] Hopkins	*Lynx canadensis*[3] Kerr		Lynx[42]	British Columbia[45]	Canada; U.S.: Utah, Colorado to West Virginia
Felicola subrostratus (Burmeister) (cat louse)[14]	*Felis silvestris* (= *catus*) Schreber		European wildcat (domestic cat)	Worldwide[16]	Europe, to S.W. China; C. India, E. Africa to South Africa; domestic cat worldwide
	Lynx rufus (Schreber)		Bobcat		Canada; U.S. to Mexico: Oaxaca
	Salanoia concolor I. Geoffroy	Herpestidae	Madagascar brown-tailed mongoose		Madagascar
	Civettictis civetta (Schreber)	Viverridae	African civet		Subsaharan Africa
Felicola sudamericanus[58] Emerson & Price	*Leopardus tigrinus* (Schreber)	Felidae	Tiger cat[58]	Colombia: Malvasi[58]	Central America, South America
Felicola zeylonicus[11] (Bedford)	*Herpestes vitticollis*[11] Bennett	Herpestidae	Striped-neck mongoose[42]	Sri Lanka: Mousakande[16]	S. India, Sri Lanka
Geomydoecus[e] (102 spp. and subspp.)	441 spp. and subspp. in order Rodentia	Geomyidae	Pocket gopher		North and Central America

[e] Pocket gopher lice were reviewed by Hellenthal and Price (1991).[62]

Order Mallophaga, suborder Ischnocera, family Trichodectidae—*Continued*

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host
Lorisicola mjobergi[11] (Stobbe)	*Nycticebus coucang*[11] (Boddaert)	Lorisidae[11]	Slow loris[42]	Indonesia: Borneo,[43] Sumatra; Malaysia	S. Philippines; S. Asia;[3] S.E. Asia; Indonesia: Sumatra, Java, Borneo
Lutridia exilis (Giebel)	*Lutra lutra* (Linnaeus)	Mustelidae	Eurasian otter	Germany, England,[16] Italy, North America	Europe; Asia; Indonesia: Java, Sumatra; N.W. Africa
Lutridia lutrae (Werneck)	*Pteronura brasiliensis* (Gmelin)		Flat-tailed otter[2]	Brazil	Streams of South America from Venezuela and the Guianas to Uruguay and N. Argentina
Lutridia matschiei (Stobbe)	*Lutra maculicollis* Lichtenstein		Spotted-necked otter[42]	Cameroon: Bipindi; Uganda: Kigezi (Lake Bunyonyi)	Africa: Liberia to Ethiopia south to South Africa except east coast and S.W. deserts
	Aonyx congicus Lönnberg		African small-clawed otter		Zaire, Congo Basin to Uganda, Niger
Lymeon cummingsi Eichler	*Bradypus tridactylus*[3] Linnaeus	Bradypodidae	Three-toed sloth	Costa Rica[43]	S. Venezuela south to the Guianas; Brazil: Amazon and Rio Negro Rivers
	Bradypus variegatus Schinz				E. Honduras to S.E. Brazil, N. Argentina, Peru, Ecuador, Colombia
Lymeon gastrodes (Cummings)	*Choloepus didactylus* (Linnaeus)		Two-toed sloth[48]	Guyana	Venzuela: Delta of and south of Rio Orinoco; Brazil: Amazon River; to Amazon, Basin of Colombia, Ecuador, Peru
Neofelicola aspidorhynchus Werneck	*Prionodon linsang* (Hardwicke)	Viverridae	Banded linsang[42]	Indonesia: Sumatra[16]	S.E. Asia; Indonesia: Sumatra, Java, Borneo
Neofelicola bengalensis Werneck	*Paradoxurus hermaphroditus* (Pallas)		Common civet	Malaysia, Thailand	Sri Lanka, India to Indonesia (Sumatra, Java, Borneo, Celebes), Philippines, Pacific Islands
Neofelicola philippinensis Emerson	*Paradoxurus philippinensis*[11] Jourdan		Philippine palm civet[63]	Philippines: Palawan,[63] Balabac	Philippines[63]
Neofelicola sumatrensis Werneck	*Prionodon linsang* (Hardwicke)		Banded linsang[42]	Indonesia: Sumatra[16]	S.E. Asia; Indonesia: Sumatra, Java, Borneo[3]
Neotrichodectes arizonae Werneck	*Conepatus leuconotus* (Lichtenstein)	Mustelidae	Texas hog-nosed skunk	Probably same as host	U.S.: S. Gulf Coast of Texas; Mexico: south along Gulf Coast to Veracruz
	Conepatus mesoleucus (Lichtenstein)		Arizona hog-nosed skunk		U.S.: S.E. Colorado south through Arizona, New Mexico, S. Texas; to N. Nicaragua
Neotrichodectes chilensis Werneck	*Conepatus chinga*[3] (Molina)		Argentine skunk	Chile, Bolivia, Argentina, Brazil	Chile, Peru, Bolivia, N. Argentina, S. Brazil, Uruguay
	Conepatus humboldtii Gray				Paraguay, N.E. Argentina south to Strait of Magellan
Neotrichodectes interruptofasciatus (Kellogg & Ferris)	*Taxidea taxus* (Schreber)		American badger	U.S.: California, Texas, Colorado	S.W. Canada to Ontario; all U.S.; Mexico: Baja California to Puebla
Neotrichodectes mephitidis (Packard)	*Mephitis macroura* Lichtenstein		Hooded skunk	Probably same as host	U.S.: S. Texas, New Mexico, Arizona; through Mexico to N. Nicaragua

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host
Order Mallophaga, suborder Ischnocera, family Trichodectidae—*Continued*					
Neotrichodectes mephitidis (Packard) ***—Continued***	*Mephitis mephitis*[11] (Schreber)	Mustelidae[11]	Striped skunk[42]		North America[3]
Neotrichodectes minutus[11] (Paine)	*Mustela frenata* Lichtenstein		Long-tailed weasel	U.S.: Illinois, California, Montana,[16] New Mexico; Mexico; Brazil	S. Canada; U.S.: all except deserts; to Venezuela and Bolivia
	Mustela nigripes (Audubon & Bachman)		Black-footed ferret		Formerly in Canada: S. Alberta and Saskatchewan; south to U.S.: Arizona, New Mexico, N.W. Texas
Neotrichodectes osborni Kéler	*Spilogale putorius* (Linnaeus)		Spotted skunk[48]	U.S.: Iowa, Arizona, California, Florida; Canada	Canada: British Columbia; most of U.S.; south through Mexico into Costa Rica
Neotrichodectes pallidus (Piaget)	*Nasua nasua*[3] (Linnaeus)	Procyonidae	Coati[42] (coatimundi)	Mexico, Panama, Colombia, Brazil, Bolivia, Paraguay	South America
Neotrichodectes semistriatus Emerson & Price	*Conepatus semistriatus* (Boddaert)	Mustelidae	Amazonian skunk	Venezuela[64]	S. Mexico to Peru and E. Brazil
Neotrichodectes thoracicus (Osborn)	*Bassariscus astutus*[11] (Lichtenstein)	Procyonidae	Cacomistle[2] or ring-tail	U.S.: California[16]	W., S.W. U.S. to S. Mexico
Neotrichodectes wolffhugeli (Werneck)	*Conepatus chinga* (Molina)	Mustelidae	Argentine skunk[42]	Chile, Bolivia	Chile, Peru, Bolivia, N. Argentina, S. Brazil, Uruguay
Parafelicola acuticeps (Neumann)	*Genetta abyssinica* (Rüppell)	Viverridae	Abyssinian genet	Ethiopia; Libya: Tripoli; South Africa: Transvaal; Tanzania	Egypt, Ethiopia, Somalia, Sudan
	Genetta genetta (Linnaeus)		Small-spotted genet		N. Africa, Near East, S. Europe
	Genetta tigrina (Schreber)		Blotched genet		South Africa, Lesotho
Parafelicola africanus Emerson & Price	*Genetta genetta* (Linnaeus)		Small-spotted genet	Egypt[65]	N. Africa, Near East, S. Europe
Parafelicola lenicornis Werneck	*Genetta tigrina* (Schreber)		Blotched genet	Congo[16]	South Africa, Lesotho
	Genetta victoriae Thomas		Giant genet[47]		E. Zaire
Parafelicola neoafricanus Emerson & Price	*Genetta tigrina* (Schreber)		Blotched genet[42]	Mozambique[66]	South Africa, Lesotho
Parafelicola viverriculae (Stobbe)	*Viverricula indica* (Desmarest)		Small Indian civet	Madagascar[16]	S. Asia; Indonesia: Sumatra,[42] Borneo; Taiwan; introduced to Madagascar
Parafelicola wernecki (Hopkins)	*Genetta thierryi*[3] Matschie (includes *G. villiersi*)		Genet	Uganda, Congo	S. Mauritania to Cameroon[3]
	Genetta tigrina[11] (Schreber)		Blotched genet		South Africa, Lesotho

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host
Order Mallophaga, suborder Ischnocera, family Trichodectidae—*Continued*					
Procavicola[f] (30 spp.)	Spp. in order Hyracoidea	Procaviidae	Hyraxes (tree and rock dassies)		Africa, Near East
Procaviphilus[f] (7 spp.)					
Stachiella divaricata[11] (Harrison)	*Galictis cuja*[3] (Molina)	Mustelidae[11]	Little grison[2]	Chile: Temulco[16]	S. South America[3]
Stachiella ermineae Hopkins	*Mustela erminea* Linnaeus (includes *M. rixosa*)		Ermine (stoat)	England, Germany, U.S., Canada	Cosmopolitan in Northern Hemisphere
Stachiella kingi (McGregor)	*Mustela rixosa*[11] (Bangs)		Weasel	U.S.: Montana, Maine, Alaska	Palearctic and Nearctic regions; Canada; U.S.: Alaska, south to Wyoming, North Carolina
Stachiella larseni Emerson	*Mustela vison* Schreber		American mink	U.S.: Alaska, Maryland, North Carolina[67]	Canada; U.S.: Alaska, contiguous states except S.W. desert areas
Stachiella mustelae (Schrank)	*Mustela nivalis* Linnaeus		Weasel	Germany: Bavaria, Switzerland;[16] Italy; England; U.S.: Montana, Maine, Alaska	Palearctic region; Japan; Canada; U.S.: Alaska, south to Wyoming, North Carolina
	Mustela sibirica Pallas		Siberian weasel		N. Palearctic region
Stachiella ovalis (Bedford)	*Ictonyx striatus* (Perry)		Zorilla	South Africa, Kenya, Uganda	Africa
Stachiella retusa jacobi Eichler	*Mustela putorius* Linnaeus		European polecat	Germany: Bremen	Europe
Stachiella retusa martis Werneck	*Martes americana* (Turton)		American marten	U.S.: California	Canada; U.S.: Alaska, south to 35° N.
Stachiella retusa retusa (Burmeister)	*Martes foina* (Erxleben)		Stone marten	Germany, Italy	Europe and Asia[42]
Stachiella retusa salfii Conci	*Martes martes* (Linnaeus)		Pine marten	Italy	Europe east to Russia: W. Siberia[3]
Stachiella ugandensis (Bedford)	*Poecilogale albinucha*[3] (Gray)		White-naped weasel	Uganda: Kigezi	Zaire, Uganda, Tanzania south to South Africa
Stachiella zorillae (Stobbe)	*Poecilictis libyca*[11] (Hemprich & Ehrenberg)		Libyan striped weasel	Tunisia: Tunis;[16] Spain: Melilla[68] (on African mainland)	N. Africa: Fringes of Sahara Desert from Morocco and Egypt to Sudan; Spain: Melilla
Suricatoecus congoensis Emerson & Price	*Crossarchus alexandri* Thomas & Wroughton	Herpestidae	Congo kusimanse[42]	Zaire[69]	Central African Republic, Congo, Uganda, Zaire
Suricatoecus cooleyi (Bedford)	*Suricata suricatta* (Schreber)		Slender-tailed suricat	South Africa: Transvaal,[16] Orange Free State	South Africa, mostly south of Orange River;[42] Angola; Namibia; S. Botswana[3]

[f]Validity of spp. and subspp. assigned to these two genera and to *Dasonyx* and *Eurytrichodectes* is uncertain and awaits clarification.[11]

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host
Order Mallophaga, suborder Ischnocera, family Trichodectidae—*Continued*					
Suricatoecus decipiens[11] (Hopkins)	*Mungos mungo*[3] (Gmelin)	Herpestidae[3]	Banded mongoose[42]	Uganda: Kampala[16]	Subsaharan Africa[3]
Suricatoecus fahrenholzi Werneck	*Cerdocyon thous* (Linnaeus) *Dusicyon fulvipes*[11] (Martin)	Canidae	Crab-eating fox Chiloe fox	Paraguay, Peru	South America: most countries north of N. Argentina Chile: Isla de Chiloé[42]
Suricatoecus guinlei Werneck	*Otocyon megalotis* (Desmarest)		African big-eared fox[2]	Kenya	E. and S. Africa to Ethiopia[3]
Suricatoecus helogale (Bedford)	*Helogale parvula parvula* (Sundevall)	Herpestidae	Dwarf mongoose[47] (pygmy mongoose)	South Africa: Transvaal (Rio N'jelele)	Somalia, Ethiopia to South Africa and Namibia
Suricatoecus helogaloidis Werneck	*Helogale parvula undulata* (Peters)		Dwarf mongoose (pygmy mongoose)	South Africa: Haullich	Subsaharan Africa
Suricatoecus hopkinsi (Bedford)	*Nandinia binotata*[3] (Gray)	Viverridae	Two-spotted palm civet	Uganda: Kampala, Kabale; Zaire: Kivu	Subsaharan Africa
Suricatoecus laticeps (Werneck)	*Atilax paludinosus* (G. Cuvier)	Herpestidae	Marsh mongoose	Tanzania	Africa
Suricatoecus mungos (Stobbe)	*Herpestes sanguineus*[22] (Rüppell)		Slender mongoose	Tanzania, Congo	Subsaharan Africa
Suricatoecus occidentalis[70] Emerson & Price	*Crossarchus obscurus* F. Cuvier		Western kusimanse[70]	Ivory Coast, Nigeria[70]	Sierra Leone to Cameroon
Suricatoecus paralaticeps[11] Werneck	*Atilax paludinosus* (G. Cuvier)		Marsh mongoose[47]	Uganda: Kampala[16]	Africa
Suricatoecus quadraticeps (Chapman)	*Urocyon cinereoargenteus* (Schreber) *Vulpes velox* (Say)	Canidae	Gray fox[42] Kit fox	Probably same as host	Most of North America[42] to N. South America S.W. Canada to U.S.: N.W. Texas, New Mexico[2]
Suricatoecus vulpis (Denny)	*Vulpes vulpes* (Linnaeus)		Red fox	Britain; India and Pakistan: Kashmir Canada; U.S.: California	N. North America to Texas,[48] New Mexico; Europe; Asia; Palearctic Africa
Thomomydoecus[g] (20 spp. and subspp.)	441 spp. and subspp. in order Rodentia	Geomyidae	Pocket gopher		North and Central America
Trichodectes barbarae[11] Neumann	*Eira barbara*[11] (Linnaeus)	Mustelidae	Tayra[79]	Brazil; Costa Rica: San Juan	Mexico through Central America to Trinidad and Tobago; through South America to Argentina
Trichodectes canis (de Geer) (dog-biting louse)[14]	*Canis aureus* Linnaeus	Canidae	Asiatic jackal[2] (golden jackal)	Worldwide	N. Africa, S.W. Asia, S.E. Europe

[g]Pocket gopher lice were reviewed by Hellenthal and Price (1991).[62]

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host
Order Mallophaga, suborder Ischnocera, family Trichodectidae—*Continued*					
Trichodectes canis (de Geer) (dog-biting louse)[14] —***Continued***	*Canis latrans*[3] Say	Canidae[11]	Coyote[42]		U.S.: Alaska south to Central America[3] and east to New York; Canada
	Canis lupus Linnaeus (includes *C. familiaris*)		Gray wolf (includes domestic dog and dingo)		Originally in North America, Europe, Asia; now eliminated from nearly all settled areas; domestic dog is cosmopolitan
	Canis rufus Audubon & Bachman		Red wolf		U.S.: Texas, Louisiana; endangered species
	Cerdocyon thous (Linnaeus)		Crab-eating fox[2]		South America: most countries north of N. Argentina
	Dusicyon culpaeus[11] (Molina)		South American fox		Along Andes mts. of Argentina; highlands of Bolivia, Peru, Colombia, Ecuador
	Vulpes bengalensis (Shaw)		Bengal fox		India, Pakistan, S. Nepal
	Civettictus civetta[3] (Schreber)	Viverridae[3]	African civet		Subsaharan Africa
Trichodectes emersoni[11] Hopkins	*Melogale orientalis* (Horsfield)	Mustelidae	Bornean ferret badger	N. Borneo[45]	Indonesia: Borneo, Java[2]
Trichodectes emeryi Emerson & Price	*Martes flavigula* (Boddaert)		Yellow-throated marten	Nepal: Sankhuwa Sabha[71]	Malaya,[48] Korea, China west to NW Pakistan,[3] Taiwan, Indonesia: Sumatra, Java, Borneo
Trichodectes fallax Werneck	*Procyon cancrivorus* (G. Cuvier)	Procyonidae	Crab-eating raccoon	Brazil: São Paulo (Guariba[16]); Argentina: Jujuy	S. Costa Rica, Panama, South America to N.E. Argentina[3]
Trichodectes ferrisi Werneck	*Tremarctos ornatus* (F. Cuvier)	Ursidae	Spectacled bear	Venezuela: Táchira (Rubio)	Mt. regions of W. Venezuela, Colombia, Ecuador, Peru, W. Bolivia, perhaps Panama
Trichodectes galictidis Werneck	*Grisonella furax*[11] (Thomas)	Mustelidae	Little grison	Brazil, Chile, Panama	S. South America
	Galictis vittata Schreber		Grison		S. Mexico, Central America, to Peru and Bolivia
Trichodectes kuntzi Emerson	*Melogale moschata* (Gray)		Bornean ferret badger	Taiwan[72]	India: Assam; C., S.E. China; N. Laos; N. Vietnam
Trichodectes malaysianus Werneck	*Cynogale bennetti* Gray	Viverridae	Otter civet	Indonesia: Sumatra[16]	Malaya; Indochina; Indonesia: Sumatra, Borneo
Trichodectes melis (J.C. Fabricius)	*Meles meles* (Linnaeus)	Mustelidae	Old World badger	Probably same as host	Europe; Asia south to China: Tibet, S. China; N. Burma;[2] Japan[42]
Trichodectes octomaculatus Paine	*Procyon lotor*[3] (Linnaeus)	Procyonidae	Raccoon[42]	Probably same as host	S. Canada through most of U.S.;[3] Central America to C. Panama
Trichodectes pinguis[73] *euarctidos* Hopkins	*Ursus americanus* Pallas	Ursidae	North American black bear	Canada: British Columbia, Ontario	Originally in wooded areas of North America north of C. Mexico
Trichodectes pinguis pinguis[11] Burmeister	*Ursus arctos* Linnaeus		Brown bear		Scarce in Europe, but in Pyrenees, Scandanavia, E. Europe, N., C. Asia; W. half of Canada; U.S.: Alaska, south through U.S. to N. Mexico

Order Mallophaga, suborder Ischnocera, family Trichodectidae—*Continued*

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host
Trichodectes potus [11] Werneck	*Potos flavus* [11] (Schreber)	Procyonidae [11]	Kinkajou [2]	Brazil: Rio de Janeiro state, Pará; [16] Venezuela: Cordillera Mérida	Forests of S. Mexico, Central America, [3] south at least to Brazil: Mato Grosso
Trichodectes vosseleri Stobbe	*Mellivora capensis* (Schreber)	Mustelidae	Honey badger	Tanzania; South Africa: Cape Province	Most of Africa; Asia [42] from Arabia to Russia: Turkestan; India
Tricholipeurus aepycerus Bedford	*Aepyceros melampus* (Lichtenstein)	Bovidae	Impala [42]	Namibia: Kunene River [43]	C., S. Africa [3] from Kenya and Uganda to South Africa
Tricholipeurus albimarginatus (Werneck)	*Mazama americana* (Erxleben)	Cervidae	Red brocket	Brazil: several states; Bolivia: Yacuiba	South America; Panama: San José Island
	Mazama gouazoubira (G. Fischer)		Brown brocket		Central and South America [42]
Tricholipeurus annectens (Hopkins)	*Tragelaphus scriptus* (Pallas)	Bovidae	Bushbuck	Uganda: Lango District	Subsaharan Africa [2]
	Tragelaphus spekei (Sclater)		Sitatunga		C. Africa [3]
Tricholipeurus antidorcas Bedford	*Antidorcas marsupialis* (Zimmermann)		Springbuck	South Africa: Onderstepoort	Botswana, Namibia (former range was more extensive)
Tricholipeurus balanicus [74] *balanicus* (Werneck)	Antilope cervicapra (Linnaeus)		Blackbuck	India; Pakistan; England: Zoological Garden of London (holotype)	W. Pakistan and India from Sind, Kathiawar, and Punjab east to Bengal and south to Cape Comorin
Tricholipeurus balanicus [11] *ourebiae* (Hopkins)	*Ourebia ourebi* (Zimmermann)		Oribi	Uganda, Sudan	Grasslands of Subsaharan Africa; [2] now rare
Tricholipeurus bedfordi (Hill)	*Cephalophus monticola* (Thunberg)		Blue duiker [47]	South Africa: Natal, Transvaal	Widely distributed [47] through C., S. Africa
Tricholipeurus clayae [74] (Werneck)	*Neotragus pygmaeus* (Linnaeus)		Royal pygmy antelope [48]	England: Zoological Garden of London; Ghana: Timang	Sierra Leone, Liberia, [2] east into Nigeria
Tricholipeurus dorcelaphi [11] (Werneck)	*Ozotoceros bezoarticus* (Linnaeus)	Cervidae	Pampas deer [42]	Brazil: Mato Grosso	Brazil, Paraguay, [3] Uruguay, Bolivia to Argentina: N. Patagonia
Tricholipeurus elongatus Bedford	*Aepyceros melampus* (Lichtenstein)	Bovidae	Impala [48]	South Africa: Transvaal; Botswana	C., S. Africa from Kenya and Uganda to South Africa
Tricholipeurus indicus Werneck	*Muntiacus muntjak* (Zimmermann)	Cervidae	Muntjak [2]	India: Manipur	Manchuria in China through Korea and Siberia to W. Mongolia
Tricholipeurus lerouxi Bedford	*Sylvicapra grimmia* (Linnaeus)	Bovidae	Gray duiker	South Africa: Zululand; Uganda: Kigezi	Most of Subsaharan Africa
Tricholipeurus lineatus (Bedford)	*Raphicerus campestris* (Thunberg)		Steinbok	South Africa: Transvaal; Kenya: Naivasha; Zambia: Abercon; probably same as host	S. Kenya, Angola, N. Tanzania, South Africa
	Raphicerus sharpei Thomas		Sharpe's grysbok		E. South Africa to Tanzania and S.E. Zaire
Tricholipeurus lipeuroides (Megnin)	*Odocoileus hemionus* (Rafinesque)	Cervidae	Mule deer [28] (black-tailed deer)	Probably same as host	W. Canada, W. U.S., south into N. Mexico [2]

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host

Order Mallophaga, suborder Ischnocera, family Trichodectidae—*Continued*

Louse	Scientific name	Family	Common name	Louse	Host
Tricholipeurus lipeuroides (Megnin) —***Continued***	*Odocoileus virginianus* (Zimmermann)		White-tailed deer[2]		S. Canada, most of U.S., south to N. South America[2]
Tricholipeurus moschatus[56] Emerson & Price	*Neotragus moschatus*[3] (Von Dueben)	Bovidae	Zanzibar antelope[48] (suni)	Kenya: Naro Motu[56]	E. Africa[42]
Tricholipeurus pakenhami[11] Werneck	*Cephalophus adersi*[11] Thomas		Zanzibar red duiker[78]	Tanzania: Zanzibar;[43] Uganda: Bunyoro District, Lango District	Tanzania: Zanzibar Island;[3] adjacent coasts of Tanzania and Kenya
	Cephalophus monticola (Thunberg)		Blue duiker[47]		Widely distributed[47] through C., S. Africa
	Sylvicapra grimmia[3] (Linnaeus)		Gray duiker[48]		Most of Subsaharan Africa[3]
Tricholipeurus parallelus (Osborn)	*Odocoileus hemionus*[11] (Rafinesque)	Cervidae	Mule deer[2] (black-tailed deer)[42]	North America[28]	W. Canada, W. U.S., south into N. Mexico[2]
	Odocoileus virginianus (Zimmermann)		White-tailed deer[2]		S. Canada, most of U.S., south to N. South America
Tricholipeurus parkeri Hopkins	*Gazella thomsoni* Günther	Bovidae	Thomson's gazelle[42]	Kenya: Naivasha[43]	S. Sudan[3] to N. Tanzania
Tricholipeurus spinifer (Hopkins)	*Gazella granti* Brooke		Grant's gazelle	Uganda: Karamoja District	Tanzania, Uganda, Kenya, Somalia, Ethiopi
Tricholipeurus trabeculae reduncae Bedford	*Redunca arundinum* (Boddaert)		Southern reedbuck	South Africa: Zululand; Malawi	S. Africa below equator
Tricholipeurus trabeculae trabeculae Bedford	*Redunca fulvorufula* (Afzelius)		Mountain reedbuck	South Africa: Zululand	S. Ethiopia, Kenya, parts of S. Africa, part of Cameroon; discontinuous
Tricholipeurus trabeculae ugandae Werneck	*Redunca redunca* (Pallas)		Bohor reedbuck[47]	Uganda: Buruli, Kigezi District	Senegal east to Ethiopia and E. Equatorial Africa
Tricholipeurus victoriae (Hopkins)	*Madoqua guentheri* Thomas		Guenther's long-snouted dik-dik	Uganda: Karamoja District; Kenya: Naivasha	Ethiopia, Somalia, Kenya, Sudan, Uganda
	Madoqua kirkii (Günther)		Kirk's dik-dik		Parts of E. Equatorial Africa, parts of S.W. Africa

Order Mallophaga, suborder Rhynchophthirina, family Haematomyzidae

Louse	Scientific name	Family	Common name	Louse	Host
Haematomyzus elephantis[11] Piaget	*Elephas maximus*[11] Linnaeus	Elephantidae[11]	Asiatic or Indian[2] elephant	Africa, S. Asia;[43] probably worldwide in zoos	Sri Lanka; India to Vietnam;[3] Malaya; Indonesia: Sumatra, Borneo
	Loxodonta africana (Blumenbach)		African elephant		Most of Subsaharan Africa but rare in South Africa; extinct in N. Africa
Haematomyzus hopkinsi Clay	*Phacochoerus aethiopicus* (Pallas)	Suidae[3]	Warthog	Uganda: Karmoja District;[75] Kenya; Meru; Ethiopia: Harrar Province[76]	Most of Subsaharan Africa
Haematomyzus porci[77] Emerson & Price	*Potamochoerus porcus*[3] (Linnaeus)		Bush pig	Ethiopia: near Addis Ababa[77]	Subsaharan Africa, Madagascar

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Appendix B. Hosts and distribution of lice in the order Anoplura[a, b]

Louse	Host			Distribution[c]	
	Scientific name	Family	Common name	Louse	Host
Order Anoplura, family Echinophthiriidae					
Antarctophthirus callorhini[1] (Osborn)	*Callorhinus ursinus*[2] (Linnaeus)	Otariidae[3]	Northern fur seal[3]	U.S.: Alaska (Pribilof Islands);[6] Pacific Ocean off west coast of Canada, Washington, Oregon, California	Bering Sea; Sea of Okhotsk;[3] Pacific Ocean; Sea of Japan; as far south as waters off U.S.: California (San Diego); and Japan
Antarctophthirus lobodontis Enderlein	*Lobodon carcinophagus*[4] (Hombron & Jacquinot)	Phocidae	Crabeater seal[4]	Antarctica: Booth Wandel Island[1]	S. Pacific Ocean to waters off South America and Australia
Antarctophthirus mawsoni Harrison	*Ommatophoca rossii* Gray		Ross seal	Antarctica: S. Shetland Islands (King George Island)	Antarctica: Circumpolar pack ice
Antarctophthirus microchir (Trouessart & Neumann)	*Eumetopias jubata*[52] (Schreber)	Otariidae	Northern or stellar sea lion[6]	U.S.: California coast; New Zealand:[6] Auckland Islands	N. Pacific Ocean[52]
	Neophoca cinerea (Peron)		Australian sea lion		S. coast of Australia
	Phocarctos hookeri (Gray)		New Zealand sea lion		Extreme S. New Zealand (subantarctic islands)
	Zalophus californianus (Lesson)		California sea lion		W. coast of North America; Ecuador: Galapagos; S. Sea of Japan
Antarctophthirus ogmorhini Enderlein	*Hydrurga leptonyx*[4] (Blainville)	Phocidae	Leopard seal[4]	Antarctica: Victoria Land, Booth Wandel Island;[1] McMurdo Sound, Wilkes Land[4]	Antarctica
	Leptonychotes weddelli (Lesson)		Weddell seal		Antarctica; occasionally seen in S. Australia, New Zealand, and South America
Antarctophthirus trichechi[6] (Bohemann)	*Odobenus rosmarus*[6] (Linnaeus)	Odobenidae	Walrus[6]	Arctic region; northern Pacific and Atlantic Oceans; U.S.: Alaska; Canada: Labrador; Norway: Spitzbergen Island[6]	Open waters of Arctic Ocean; Russia: N.E. coast of Siberia; U.S.: N.W. coast of Alaska; N.W. Greenland; Canada: Ellesmere Island
Echinophthirus horridus (von Olfers)	*Cystophora cristata* (Erxleben)	Phocidae	Hooded seal	Northern Hemisphere, probably same as hosts	N. Atlantic and Arctic Oceans from Canada: Newfoundland to USSR: Novaya Zemlya
	Erignathus barbatus (Erxleben)		Bearded seal		Circumpolar region: coasts and islands
	Halichoerus grypus (Fabricius)		Gray seal		N. Atlantic from Labrador east to Russia: Novaya Zemlya and south to Great Britain: Channel Islands; France
	Phoca groenlandica[6, 52] Erxleben		Harp seal		N. Atlantic Ocean and adjoining waters of Arctic Ocean

[a]Superscript numbers indicate references listed at end of appendix B. Where no superscript appears, the last number above applies.
[b]Where no item appears in a column, the last item above applies.
[c]Authors used current names for geographical entries in cols. 5 and 6. However, references for this appendix may use out-of-date geographical names.

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host
Order Anoplura, family Echinophthiriidae—*Continued*					
Echinophthirus horridus (von Olfers) ***—Continued***	*Phoca hispida*[52] Schreber		Ringed seal[6]		Arctic Ocean; lakes of W. Europe and Canada: Baffin Island
	Phoca sibirica Gmelin		Baikal seal[5]		Russia: E. Siberia (Lake Baikal)
	Phoca vitulina Linnaeus		Harbor seal[3]		Shores of oceans of Northern Hemisphere
Latagophthirus rauschi[6] Kim & Emerson	*Lutra canadensis*[6] (Schreber)	Mustelidae[3]	Canadian otter	U.S.: Oregon (Coos County[6]), Alaska (Baranof Island)	Canada and U.S.:[52] Alaska and Pacific Coast, south to Texas and Arizona
Lepidophthirus macrorhini[7] Enderlein	*Mirounga leonina*[52] (Linnaeus)	Phocidae	Southern elephant seal[5]	France: Iles Kerguélen; South Africa: near Cape Town;[1] Australia: Macquarie Island[7]	Antarctic islands; Argentina; United Kingdom: Falkland Islands, Gough Island; Australia: Macquarie Island
Lepidophthirus piriformis[8] (Blagoveschensky)	*Monachus monachus*[8] (Hermann)		Monk seal[8]	USSR: Black Sea coast[8]	Black and Mediterranean[52] Seas; N.W. Africa to Tunisia: Cape Blanc
Proechinopthirus fluctus[55] (Ferris)	*Callorhinus ursinus*[6] (Linnaeus)	Otariidae	Northern fur seal[6]	U.S.: Alaska (St. Paul Island,[6] Pribilof Islands), Washington to Oregon; coast of Canada	(See above)
	Eumetopias jubata (Shreber)		Northern or stellar sea lion		N. Pacific Ocean
Proechinopthirus zumpti (Werneck)	*Arctocephalus pusillus*[9] (Shreber)		Cape fur seal[9]	South Africa: Cape Province[9]	Sea and islands along S. coast of Africa
Order Anoplura, family Enderleinellidae					
Atopophthirus emersoni[10] Kim	*Petaurista elegans*[10] (Müller)	Sciuridae[11]	Lesser giant flying squirrel[10]	Malaysia: Johor,[10] Mersing	Indonesia: Java;[11] Malaysia: Johor
Enderleinellus arizonensis[1] Werneck	*Sciurus alleni*[1] Nelson		Allen's squirrel[12]	U.S.: Arizona[1] (Huachuca Mts.); Mexico: Chihuahua (Colonia Garcia), Zacatecas, Sierra Madre, Sierra Guadalupe	N.E. Mexico: Coahuila,[12] Nuevo Leon, Tamaulipas to San Luis Potosi
	Sciuris arizonensis Coues		Arizona gray squirrel		U.S.: Arizona, W. New Mexico; Mexico: Sonora
	Sciurus nayaritenis J.A. Allen		Nayarit squirrel		Mexico: Chihuahua, Sonora, Durango (Sierra Madre Mts.)
Enderleinellus brasiliensis Werneck	*Sciurus aestuans* Linnaeus		Tropical red squirrel	Brazil: Abaete, Pará	South America: Venezuela to N. Argentina

Louse	Host			Distribution	
	Scientific name	Family	Common name	Louse	Host

Order Anoplura, family Enderleinellidae—*Continued*

Louse	Scientific name	Family	Common name	Distribution: Louse	Distribution: Host
Enderleinellus deppei[13] Kim	*Sciurus deppei*[12] Peters	Sciuridae[3]	Deppe's squirrel[12]	Mexico: Tabasco,[13] Oaxaca; Costa Rica: Guanacarte (Santa Clara)	Mexico: Tamaulipas to Chiapas;[12] Central America to Costa Rica
	Sciurus granatensis Humboldt		Tropical red squirrel		Costa Rica to N. South America
Enderleinellus dremomydis[1] Ferris	*Dremomys pernyi*[1] (Milne-Edwards)		Perny's long-nosed squirrel	China: W. Sichuan[1]	Burma and Tibet to C.[52] and S.E. China, Taiwan
Enderleinellus euxeri Ferris	*Xerus erythropus*[55] (Desmarest)		Striped ground squirrel[14]	Tanzania: Oni, Wambugu;[1] Dahomey: Diho; Nigeria: Sokoto[55]	Forest region of W. Africa,[14] from Mauritania across Africa to S.W. Ethiopia and Kenya
Enderleinellus extremus Ferris	*Sciurus aureogaster* Cuvier		Red-bellied squirrel[12]	Guatemala: Nenton;[1] Mexico: Tamaulipas, Veracruz, Oaxaca, Tabasco, Chiapas	Guatemala; Mexico: to Nayarit,[52] Guanajuato, Nuevo Leon
	Sciurus deppei Peters		Deppe's squirrel		Mexico: Tamaulipas to Chiapas; Central America to Costa Rica
Enderleinellus heliosciuri Ferris	*Heliosciurus gambianus*[52] (Ogilby)		Gambian sun squirrel[16]	Uganda, Congo (Ruwenzori Mts.), Kenya	Africa: Senegal to Ethiopia[14]
	Heliosciurus ruwenzorii (Schwann)		Ruwenzori sun squirrel[14]		E. Congo, W. Uganda, Rwanda, Burundi, E. Zaire
	Protoxerus stangeri (Waterhouse)		African giant squirrel		Africa: Sierra Leone[16] to Tanzania and Angola
Enderleinellus hondurensis Werneck	*Sciurus variegatoides* Ogilby		Variegated squirrel[12]	Mexico: Chiapas; Honduras: San Pedro Sula;[55] Panama: Boquerón	Mexico: Chiapas (Pacific coast);[12] through Central America to Panama
Enderleinellus insularis Werneck	*Sciurus granatenis*[55] Humboldt		Tree squirrel[11]	Venezuela: Margarita Island[1]	Costa Rica to Ecuador, Venezuela,[52] Trinidad, Tobago
Enderleinellus kaibabensis[13] Kim	*Sciurus aberti* Woodhouse		Abert's squirrel	U.S.: Arizona[55]	S.W. U.S.: Arizona[12] (Kaibab Plateau), adjoining states; N.W. Mexico
Enderleinellus kelloggi[1] Ferris	*Sciurus griseus* Ord		Western gray squirrel[12]	Western North America	U.S.: W. coast; into Mexico: Baja California Norte
Enderleinellus krochinae[13] Blagoveshchensky	*Sciurus anomalus* Guldenstaedt		Persian squirrel	N. Syria; Russia: Azerbaijan,[13] Zakataly	Turkey; Russia:[52] Transcaucasia; N., W. Iran; Syria; Israel
Enderleinellus kumadai[17] Kaneko	*Callosciurus erythraeus* (Pallas)		Passall squirrel	Japan: Tokyo[17] (Zoological Garden); Indonesia: N. Borneo; Malaysia: Selangor; Thailand: Nakhon, Sawan, Chaiyaphum provinces	Most of S.E. Asia; India;[11] Burma; S.E. China; Malaysia; Indonesia

Order Anoplura, family Enderleinellidae—*Continued*

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host
Enderleinellus kumadai[17] Kaneko —*Continued*	*Callosciurus finlaysoni*[5] (Horsfield)	Sciuridae[3]	Finlayson's squirrel[5]		Thailand, Laos, Vietnam[52]
	Callosciurus nigrovittatus[55] (Horsfield)		Malayan squirrel[3]		Malaysia; Indonesia: Sumatra, Java, Borneo
	Callosciurus notatus[17] (Boddaert)		Beautiful squirrel		Indonesia, south of Sulawesi
	Callosciurus prevosti (Desmarest)		Prevost's squirrel[5]		Malaysian subregion except Java and Sulawesi
	Glyphotes simus Thomas		Pygmy squirrel[17]		Malaysia; Indonesia: Borneo
Enderleinellus larisci[1] Ferris	*Lariscus insignis* (F. Cuvier)		Striped oriental ground squirrel	Indonesia: Lanchut, S.W. Borneo[1]	Malaysia; Indonesia: Sumatra, Borneo, Java, smaller adjacent islands
Enderleinellus longiceps Kellogg & Ferris	*Sciurus aberti*[5] Woodhouse		Abert's squirrel	U.S.: Widespread, probably same as hosts; Mexico: Chihuahua, Veracruz	S.W. U.S.: Arizona[12] (Kaibab Plateau), adjoining states; N.W. Mexico
	Sciurus alleni Nelson		Allen's squirrel[12]		N.E. Mexico: Coahuila, Nuevo Leon, Tamaulipas to San Luis Potosi
	Sciurus caroliensis Gmelin		Gray squirrel[5]		E. U.S. to Canada: Saskatchewan; introduced into W. North America and Great Britain[52]
	Sciurus niger Linnaeus		Fox squirrel[12]		U.S.: Texas north and east to Atlantic coast; adjacent Mexico; Canada: Manitoba east to Atlantic coast
	Sciurus oculatus[12] Peters		Peter's squirrel		C. Mexico
Enderleinellus malaysianus Ferris	*Callosciurus caniceps*[3] (Gray)		Golden-backed squirrel[3]	Burma: Mergui Archipelago;[17] Indonesia: Borneo; Thailand	Thailand; peninsular Burma; Malaya; adjacent islands
	Callosciurus prevosti (Desmarest)		Prevost's squirrel		(See above)
Enderleinellus marmotae Ferris	*Marmota monax*[55] (Linnaeus)		Woodchuck	U.S.: Widespread, probably same as host[55]	U.S.: Alaska, N.E. and C. areas[12] to Arkansas; Canada
Enderleinellus menetensis Ferris	*Menetes berdmorei*[5] (Blyth)		Berdmore's squirrel	Thailand: Ko Kut Island[1]	Burma, Thailand,[11] Cambodia, Vietnam, Malaysia, and nearby islands; China: Yunnan
Enderleinellus mexicanus Werneck	*Sciurus aureogaster* Cuvier		Red-bellied squirrel[12]	Mexico: Morelos, Jalisco (Chapala)	(See above)
	Sciurus colliaei Richardson		Sonoran squirrel		N.W. Mexico[52]

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host
Order Anoplura, family Enderleinellidae—*Continued*					
Enderleinellus microsciuri[1] Werneck	*Microsciurus mimulus*[1] (Thomas)	Sciuridae[3]	American pygmy squirrel[12]	Colombia, Panama[55]	Ecuador, W. Colombia,[52] Panama
Enderleinellus nannosciuri Ferris	*Nannosciurus melanotis* (Müller)		Oriental pygmy squirrel	Indonesia: Djakarta	Indonesia: Java, Borneo, Sumatra
Enderleinellus nayaritensis[13] Kim	*Sciurus nayaritensis*[13] J.A. Allen		Nayarit squirrel	Mexico: Zacatecas,[13] Sinaloa	Mexico: Chihuahua, Sonora, Durango (Sierra Madre Mts.); to S.E. Arizona
Enderleinellus nishimarui[20, 55] Kaneko	*Funambulus pennanti*[55] Wroughton		Northern palm squirrel[3]	India: Madhya Pradesh State;[55] Nepal	India, Nepal, Pakistan, E. Iran
Enderleinellus nitzschi[1] Fahrenholz	*Sciurus anomalus*[5] Gul-denstaedt		Persian squirrel[5]	Almost all Europe where hosts are found; Syria	Turkey; Russia: Transcaucasia; N., W. Iran; Syria; Israel
	Sciurus vulgaris Linnaeus		European red squirrel		Most of Palearctic region
Enderleinellus oculatus[13] Kim	*Sciurus oculatus*[12] Peters		Peter's squirrel	Mexico: Veracruz,[13] Chihuahua (Sierra Guadalupe)	C. Mexico
	Sciurus alleni Nelson		Allen's squirrel		N.E. Mexico: Coahuila,[12] Nuevo Leon, Tamaulipas to San Luis Potosi
Enderleinellus osborni[1] Kellogg & Ferris	*Spermophilus beecheyi*[52] (Richardson)		California ground squirrel[12]	U.S.: California,[1] Arizona, Texas	U.S.: Washington,[52] Oregon; to Mexico: Baja California Norte
	Spermophilus mohavensis Merriam		Mohave ground squirrel		U.S.: California (N.W. Mojave Desert, Owens Valley)
	Spermophilus tereticaudus Baird		Round-tailed ground squirrel		U.S.: Deserts of S. Nevada through California, Arizona; Mexico: Sonora
	Spermophilus variegatus (Erxleben)		Rock squirrel		U.S.: W. Texas to S. Nevada, Utah; Mexico: N. Mexico to Puebla
Enderleinellus paralongiceps[13] Kim	*Sciurus aberti*[13] Woodhouse		Abert's squirrel	U.S.: Colorado (Estes Park[13]), Arizona	S.W. U.S.: Arizona[12] (Kaibab Plateau), adjoining states; N.W. Mexico
Enderleinellus platyspicatus[1] Ferris	*Funambulus palmarum* (Linnaeus)		Indian striped palm squirrel[5]	Sri Lanka[1]	Sri Lanka; peninsular India,[11] north to Bihar
Enderleinellus pratti[13] Kim	*Sciurus colliaei*[13] Richardson		Sonoran squirrel[12]	Mexico: Nayarit (Tepic)[13]	N.W. Mexico[12]
Enderleinellus sciurotamiasis[1] Ferris	*Sciurotamias davidianus*[52] (Milne-Edwards)		Pere David's Rock squirrel[3]	China: Shensi Province[1]	N. China[3]
Enderleinellus suturalis[6] (Osborn)	*Ammospermophilus harrisii*[6, 52] (Audubon & Bachman)		Harris' antelope squirrel[12]	W. Canada and U.S.[6]	U.S.: Arizona, S.W. New Mexico;[52] Mexico: Sonora
	Ammospermophilus nelsoni[12] (Merriam)		Nelson's antelope squirrel		U.S.: S. California[12]
	Cynomys leucurus[6, 52] Merriam		Whitetail prairie dog		U.S.: W. Wyoming, N.E. Utah,[52] N.W. Colorado, S.C. Montana

Louse	Host			Distribution	
	Scientific name	Family	Common name	Louse	Host

Order Anoplura, family Enderleinellidae—*Continued*

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host
Enderleinellus suturalis[6] (Osborn) ***—Continued***	*Spermophilus beldingi*[6, 52] Merriam	Sciuridae[3]	Belding's ground squirrel[12]		U.S.: Portions of Oregon,[52] California, Nevada, Idaho, N.W. Utah
	Spermophilus elegans[52] Kennicott				U.S.: Portions of Oregon, Idaho, Nevada to Colorado and Nebraska
	Spermophilus franklinii (Sabine)		Franklin's ground squirrel		U.S.: West of Great Lakes; north into Canada
	Spermophilus lateralis (Say)		Golden-mantled ground squirrel		Canada: British Columbia, Alberta; U.S.: W. states
	Spermophilus madrensis (Merriam)		Sierra Madre mantled ground squirrel		Mexico: Chihuahua
	Spermophilus mexicanus (Erxleben)		Mexican ground squirrel		U.S.: S. New Mexico, W. Texas; Mexico: N.E. states, C. states
	Spermophilus richardsonii (Sabine)		Richardson's ground squirrel		U.S.: N.C. states; Canada: Alberta, Saskatchewan, Manitoba
	Spermophilus spilosoma Bennett		Spotted ground squirrel		U.S.: S. Texas to S.W. South Dakota, N.W. Arizona; Mexico: N.C. states
	Spermophilus tereticaudus Baird		Round-tailed ground squirrel[12]		U.S.: Deserts of S. Nevada through California, Arizona; Mexico: Sonora
	Spermophilus townsendi Bachman		Townsend's ground squirrel		U.S.: N.W. states
	Spermophilus tridecemlineatus (Mitchill)		Thirteen-lined ground squirrel		U.S.: Great Plains from C. Texas to North Dakota; S.C. Canada
	Tamiasciurus douglasii (Bachman)		Douglas' squirrel		U.S.: Mountains of Washington, Oregon, and California; Canada: S.W. British Columbia
Enderleinellus tamiasciuri[13] Kim	*Tamiasciuru hudsonicus* (Erxleben)		Red squirrel[12]	U.S.: Alaska[13] to Pennsylvania, Rhode Island, Colorado, California; Canada: Ontario	U.S.: All except S.E. states;[12] Canada: South of the tundra
Enderleinellus urosciuri[1] Werneck	*Sciurus igniventris*[5] Wagner		Tree squirrel[3]	Brazil: Rio Negro,[1] Amazonas	N.W. Brazil, S.E. Colombia,[52] S. Venezuela
Enderleinellus venezuelae Ferris	*Sciurus gerrardi*[1] Gray		Varicolored squirrel[12]	Venezuela[55]	Venezuela[13]
	Sciurus griseogena (Gray)		Venezuelan gray squirrel		Venezuela, Colombia-Venezuela[12] boundary
Enderleinellus zonatus Ferris	*Paraxerus ochraceus*[52] (Huet)		Olive scrub squirrel[5] (Huet's squirrel)	Kenya: Kijabe, Mt. Lolokroi;[56] South Africa: Zululand	S. Kenya and most of Kenya mountain forest[14] to S. Sudan and Ethiopia

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host
Order Anoplura, family Enderleinellidae—*Continued*					
Microphthirus uncinatus[6] (Ferris)	*Glaucomys sabrinus*[6] (Shaw)	Sciuridae[3]	Northern flying squirrel[6]	U.S.: California (Yosemite National Park[6]), Minnesota; Canada: British Columbia	U.S.: S. Alaska, much of N. states,[12] Appalachian and Rocky Mts.; most of Canada
	Glaucomys volans[12] (Linnaeus)		Southern flying squirrel		U.S.: E. states to E. Texas; Mexico: C. highlands; to Honduras
Phthirunculus sumatranus[19] Kuhn & Ludwig	*Petaurista petaurista*[19, 52] (Pallas)		Common giant flying squirrel[18]	Indonesia: Sumatra[19] (Deli Province)	India to Indonesia:[18] Java; north to China, Taiwan
Werneckia minuta[1] (Werneck)	*Paraxerus ochraceus*[14, 52] (Huet)		Olive scrub squirrel[5] (Huet's squirrel)	Kenya: Kijabe[1]	(See above)
Werneckia paraxeri (Werneck)	*Paraxerus palliatus*[5] (Peters)		Red-bellied squirrel[14]	Kenya, Namibia[55]	South Africa:[16] Natal; north to Somalia
Order Anoplura, family Haematopinidae					
Haematopinus acuticeps[1] Ferris	*Equus burchelli*[5] (Gray)	Equidae[16]	Burchell's zebra[16] (common zebra)	Tanzania (Tanganyika[1])	Subsaharan Africa,[16] S. Botswana to S. Africa (Orange River); *E. burchelli burchelli* probably now extinct
Haematopinus apri[1, 22] Goureau	*Sus scrofa* Linnaeus	Suidae[5]	Wild boar,[5] domestic hog	W. Europe, including Poland[3]	Europe; Asia: E. to C. Asia;[52] domesticated worldwide
Haematopinus asini[1] (Linnaeus)	*Equus asinus*[52] Linnaeus	Equidae	Domestic donkey,[3] wild ass	Worldwide[6]	Formerly N.W. Algeria,[14] adjacent Morocco and Tunisia; Egypt; N.E. Sudan; perhaps Arabia; survives only in N.E. Ethiopia and N. Somalia; domesticated worldwide
	Equus caballus[6] Linnaeus		Domestic horse		Worldwide[3]
Haematopinus breviculus[1, 22] Fahrenholz	*Taurotragus oryx*[52] (Pallas)	Bovidae	Eland[5]	Uganda[55]	Subsaharan Africa[52]
Haematopinus bufali[1] (de Geer)	*Syncerus caffer* (Sparrman)		African buffalo	South Africa: Cape of Good Hope;[1] Malawi; Zaire; Congo-Uganda: shores of Lake Edward	
Haematopinus channabasavannai[23] Rao, Khuddus, & Kuppuswamy	*Bos indicus*[23] Linnaeus		Zebu cattle[3]	India: Karnataka (Mandya)[23]	Native to India; now worldwide[3]

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host
Order Anoplura, family Haematopinidae—*Continued*					
Haematopinus eurysternus[21] (Nitzsch)	*Bos indicus*[5] Linnaeus	Bovidae[3]	Zebu cattle[3]	Worldwide[55]	Native to India; now worldwide[3]
	Bos taruus Linnaeus		European cattle		Worldwide
	Boselaphus tragocamelus[20] (Pallas)		Nilgai		Peninsular India originally; now found[52] in exotic animal parks worldwide
Haematopinus gorgonis[24] Werneck	*Connochaetes taurinus*[52] (Burchell)		Blue wildebeest[16] (brindled gnu)	Tanzania: Ukerewe Peninsula[24]	Tanganyika, Kenya through N. South Africa
Haematopinus latus[1] Neumann	*Potamochoerus porcus*[5] (Linnaeus)	Suidae	African bush pigs[3]	Malawi: Koparo;[1] Zambia: Luangwa Valley; South Africa: Zululand	Subsaharan Africa, Madagascar
Haematopinus longus[25] Neumann	*Cervus unicolor* Kerr	Cervidae	Sambar deer	India; Nepal: Kota; Cambodia	Indian subcontinent; S.E. Asia;[18] to Taiwan and Philippines
Haematopinus ludwigi[22] Weisser	*Sus barbatus*[22] Müller	Suidae	Bornean pig[22]	Malaysia: Borneo (Sarawak);[22] Philippines: Luzon (Mt. Makiling)	Malaysia; Malaya; Indonesia: Java,[22] Borneo, Sumatra; Philippines: Palawan; neighboring small islands
	Sus verrucosus[52] Müller		Javan warty pig		Malaysia, Indonesia to Philippines
Haematopinus meinertzhageni[25] Werneck	*Hylochoerus meinertzhageni* Thomas		Giant forest hog[16]	Uganda: Ankole[25]	Equatorial C. Africa[16]
Haematopinus nigricantis[26] Weisser & Kim	*Cervus nigricans*[26] Brooke	Cervidae[16]	Luzon deer[3]	Philippines: Luzon (Bontoc), Mindoro (Mt. Alan)[26]	Philippines[26]
Haematopinus oryx[27] Fiedler & Stampa	*Oryx gazella*[27] (Linnaeus)	Bovidae[3]	Gemsbok[16]	Namibia,[27] Angola[55]	S.W. Africa[16]
Haematopinus phacochoeri[1] Enderlein	*Phacochoerus aethiopicus*[5] (Pallas)	Suidae[5]	Warthog[5]	Tanzania: Mt. Kilimanjaro,[1] Akamanja, N. Myassa; South Africa: Zululand	South Africa: Cape Province; N. Kenya; Somalia[52]
Haematopinus quadripertusus[21] Fahrenholz	*Bos taurus* Linnaeus	Bovidae[3]	European cattle[3]	S. U.S.; widespread in tropical areas of world[21]	Worldwide[3]
	Bos indicus Linnaeus		Zebu cattle		Native to India; now worldwide
Haematopinus suis[1] (Linnaeus)	*Sus scrofa*[3] Linnaeus (may be hybridized)	Suidae	Wild boar,[5] domestic hog	Worldwide[55]	Worldwide
	Sus cristata Wagner		Indian wild boar[5]		India[18]
Haematopinus taurotragi Cummings	*Taurotragus oryx*[52] (Pallas)	Bovidae	Eland	South Africa; a menagerie in England[1]	Subsaharan Africa[52]

Appendix B. Hosts and distribution of lice in the order Anoplura—*Continued*

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host
Order Anoplura, family Haematopinidae—*Continued*					
Haematopinus tuberculatus[1] (Burmeister)	*Bubalus bubalis*[55] (Linnaeus)	Bovidae[3]	Asiatic water buffalo[3]	Warmer regions of world,[21] wherever water buffalo are kept. Occasionally collected from cattle, especially if maintained with water buffalo. Not in North America.	India to Indochina; introduced to[52] S.E. Asia, S. Europe, N. Africa, Australia, E. South America, Philippines, other Pacific Islands
	Bos grunniens[5] Linnaeus		Yak[5]		Tibet and adjacent countries in C. Asia
	Bos indicus Linnaeus		Zebu cattle		Native to India; now worldwide[3]
	Bos taurus Linnaeus		European cattle		Worldwide
	Camelus dromedarius Linnaeus	Camelidae	Arabian camel (dromedary)[18] (questioned by Kim & Ludwig 1978)		Originally N. Africa and Middle East[52] countries; cosmopolitan by introduction
Order Anoplura, family Hamophthiriidae					
Hamophthirius galeopitheci[28] Mjöberg	*Cynocephalus variegatus*[28] (Audebert)	Cynocephalidae[3]	Gliding lemur[3]	Malaysia: Sabah,[28] Jesselton (Ranau)	Indochina to Indonesia:[3] Java, Borneo
Order Anoplura, family Hoplopleuridae, subfamily Hoplopleurinae[29]					
Hoplopleura[d] (117 spp.)	Spp. in orders Rodentia, Lagomorpha	Muridae, Echimyidae, Sciuridae, Ochotomidae			
Pterophthirus[d] (5 spp.)		Caridae, Echimyidae			
Order Anoplura, family Hoplopleuridae, subfamily Haematopinoidinae[29]					
Ancistroplax[d] (2 spp.)	Spp. in order Insectivora	Soricidae			
Haematopinoides[d] (1 sp.)		Talpidae			
Schizophthirus[d] (7 spp.)	Spp. in order Rodentia	Dipodidae, Myoxidae			

[d]Hoplopleuridae need revision worldwide because many spp. were described from only one or two collections and have not been collected since they were described.

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host

Order Anoplura, family Hybophthiridae

Louse	Scientific name	Family	Common name	Distribution: Louse	Distribution: Host
Hybophthirus orycteropodis[29] Enderlein	*Orycteropus afer*[5] (Pallas)	Orycteropodidae[29]	Aardvark[29]	Namibia: Gochas;[1] South Africa	Most of Africa[3] south of Sahara and Sudan

Order Anoplura, family Linognathidae

Louse	Scientific name	Family	Common name	Distribution: Louse	Distribution: Host
Linognathus aepycerus[1] Bedford	*Aepyceros melampus*[5] (Lichtenstein)	Bovidae[5]	Impala[5]	South Africa between Pretoria and Johannesburg[1]	C. and S. Africa[16] from Kenya and Uganda to N. South Africa
Linognathus africanus Kellogg & Paine	*Capra hircus* Linnaeus		Domestic goat	South Africa,[1, 6] Ethiopia, India, U.S., worldwide in subtropical climates	Worldwide
	Ovis aries Linnaeus		Domestic sheep		
	Odocoileus hemionus (Rafinesque)	Cervidae	Mule deer		W. Canada, W. U.S.,[3] to N. Mexico
	Odocoileus virginianus (Zimmermann)		White-tailed deer		S. Canada, most of U.S., to N. South America
Linognathus albifrontis[30] Fiedler & Stampa	*Damaliscus albifrons*[30] (Burchell)	Bovidae	Blesbok[30]	South Africa: Orange Free State Game Reserve[30]	South Africa[18]
Linognathus angasi[31] Weisser & Ledger	*Tragelaphus angasi*[31] Gray		Nyala[31]	South Africa: Natal,[31] Zululand	S. Africa: N.E. Natal,[31] E. Transvaal, Zimbabwe, S. Malawi
Linognathus angulatus[1] (Piaget)	*Cephalophus nigrifrons*[5] Gray		Black-fronted duiker[5]	No locality given;[1] probably Netherlands: Zoological Garden of Rotterdam	W. equatorial Africa[16]
Linognathus antidorcitis[30] Fiedler & Stampa	*Antidorcas marsupialis* (Zimmermann)		Springbok	South Africa: N. Transvaal[30]	Botswana and Namibia:[52] Kalahari Desert; S. Angola; South Africa formerly, now scarce
Linognathus bedfordi[1] Ferris	*Antidorcas marsupialis* (Zimmermann)			South Africa: Onderstepoort[1]	
Linognathus breviceps (Piaget)	*Cephalophus maxwelli*[52] (H. Smith)		Blue duiker[16]	South Africa: Zululand, Transvaal	W. coast of Africa: Senegal and Gambia to Kenya and Congo
	Sylvicapra grimmia (Linnaeus)		Gray duiker		Subsaharan Africa except lowlands of Zaire Basin
Linognathus brevicornis (Giebel)	*Giraffa camelopardalis*[5] (Linnaeus)	Giraffidae	Giraffe	From captive animals in Europe;[5] Kenya; Tanzania; Tanganyika	Senegal to Somalia to South Africa to S. Angola
Linognathus cervicaprae[5] (Lucas)	*Antilope cervicapra*[50] (Linnaeus)	Bovidae	Blackbuck[5]	France: Paris Zoo; England: Zoological Garden of London	S.W. Pakistan: Sind; India:[3] Kāthiāwār, Punjab, to Bengal and to Cape Comorin

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host
Order Anoplura, family Linognathidae—*Continued*					
Linognathus damaliscus[1] Bedford	*Damaliscus albifrons*[3] (Burchell)	Bovidae[5]	Blesbok[3]	South Africa: Zoological Garden[1] of Johannesburg, Bredasdorp	South Africa[18]
	Damaliscus dorcas (Pallas)		Bontebok		South Africa: S.W. Cape Province[52] to E. Transvaal; now only in captivity
Linognathus digitalis[32] Kleynhans	*Antidorcas marsupalis*[5] (Zimmermann)		Springbok[5]	South Africa: Cape Province[32]	(See above)
Linognathus elblae[33] Benoit	*Cephalophus spadix*[33] True		Abbott's duiker[16]	Rwanda: Uinka[33]	Tanzania (higher elevations)[16]
Linognathus fahrenholzi[1] Paine	*Redunca arundinum*[52] (Boddaert)		Reedbuck[5]	South Africa: Zululand (Mfongosi);[1] Malawi: Marimba District; Mozambique[55]	South Africa to Gabon[52] and Zaire; Tanzania; Zambia; Mozambique
	Redunca fulvorufula (Afzelius)		Mountain reedbuck		Discontinuous in Africa to South Africa
Linognathus fenneci[27] Fiedler & Stampa	*Vulpes zerda* (Zimmermann)	Canidae	Desert fox[3]	Egypt[27]	Morocco to Arabia, discontinuous
Linognathus fractus[1] Ferris	*Tragelaphus scriptus* (Pallas)	Bovidae	Bushbuck	South Africa:[1] Onderstepoort	Most of Subsaharan Africa[16] except S.W. Africa
Linognathus gnu Bedford	*Connochaetes gnou*[5] (Zimmermann)		Black wildebeest[5]	South Africa: Orange Free State (Clocolan), N. Transvaal	South Africa: Orange Free State,[52] S. Transvaal to Cape Province; almost extinct
	Connochaetes taurinus (Burchell)		Brindled gnu		S. Angola, Namibia, N. South Africa, Botswana; C. Mozambique and E. Zambia to N.E. Tanzania and Kenya
Linognathus gonolobatus[31] Weisser & Ledger	*Hippotragus equinus*[31, 52] (Desmarest)		Roan antelope[31]	South Africa: Kruger National Park[31]	Most of Africa south of Sahara; discontinuous distribution
Linognathus hippotragi[1] Ferris	*Hippotragus niger*[5] (Harris)		Sable antelope[5]	South Africa:[1] Johannesburg	Kenya to South Africa, N. Botswana, Angola
Linognathus hologastrus Werneck	*Connochaetes taurinus* (Burchell)		Brindled gnu	Namibia: Grootfontein	(See above)
Linognathus kimi Van der Merwe	*Raphicerus sharpei*[52] Thomas		Cape grysbok[16]	Zimbabwe: Chipinda[55]	South Africa below Zambezi River[16]
Linognathus lewisi[1] Bedford	*Gazella thomsoni*[5] Günther		Thomson's gazelle	Kenya: Naivasha[1]	Sudan to Tanzania[52]
Linognathus limnotragi Cummings	*Tragelaphus spekii*[52] Sclater		Situtunga	England: Zoological Garden of London;[1] South Africa: Onderstepoort, Pretoria; Mozambique[37]	Most of equatorial Africa[16]

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host
Order Anoplura, family Linognathidae—*Continued*					
Linognathus limnotragi Cummings **—*Continued***	*Tragelaphus scriptus*[52] (Pallas)	Bovidae[5]	Bushbuck[3]		Most of Subsaharan Africa[16] except S.W. Africa
Linognathus nesotragi[37] Van der Merwe	*Neotragus moschatus*[16] Von Dueben		Suni[16]	Mozambique: Tete District[37]	Africa: E. coast below equator
Linognathus nevilli[34] Ledger	*Aepyceros melampus*[34] (Lichtenstein)		Impala[34]	South Africa: Loskop Dam Nature Reserve[34] (Transvaal)	C. and S. Africa[16] from Kenya and Uganda to N. South Africa
Linognathus oviformis[1] (Rudow)	Capra hircus (probably)[1] Linnaeus		Domestic goat[5]	Unknown[1]	Worldwide[3]
Linognathus ovillus (Neumann)	*Ovis aries*[5] Linnaeus		Domestic sheep	Worldwide;[35] rare; cold and temperate climates[55]	Worldwide
Linognathus panamensis[36] Ewing	*Odocoileus virginianus*[36] *chiriquensis* (J.A. Allen) (accidental)	Cervidae	Panamanian white-tailed deer[36]	U.S.: Washington, DC (National Zoological Park);[36] S. Africa[55]	Panama[36]
	Tragelaphus scriptus (Pallas) (natural)	Bovidae	Bushbuck[5]		Most of Subsaharan Africa[16] except S.W. Africa
Linognathus pedalis[1] (Osborn)	*Oreamnos americanus*[38] (Blainville)		Mountain goat[3]	U.S., South America,[1] New Zealand, Australia, South Africa	U.S. and Canada:[18] Rocky Mts. from Montana to Alaska
	Ovis aries[5] Linnaeus		Domestic sheep[5]		Worldwide
Linognathus peleus Bedford	*Pelea capreolus*[16] (Forster)		Vaal rhebok[16]	South Africa:[1] Onderstepoort	South Africa: Cape Province[16] to Natal and Transvaal
Linognathus petasmatus Ferris	*Antilope* sp.[1] (species unknown)		"North African antelope"[1]	England: Zoological Garden of Manchester[1]	Unknown[1]
Linognathus pithodes Cummings	*Antilope cervicapra*[5] (Linnaeus)		Blackbuck[5]	India; England: Zoological Garden of London	W. Pakistan and India[3]
Linognathus raphiceri[30] Fiedler & Stampa	*Raphicerus campestris* (Thunberg)		Steenbok[30]	South Africa: Cape Province,[30] Transvaal	Angola to South Africa[16] to S. Kenya
	Aepyceros melampus (Lichtenstein)		Impala		(See above)
Linognathus reduncae Fiedler & Stampa	*Redunca fulvorufula*[30] (Afzelius)		Mountain reedbuck	South Africa: Cape Province,[30] Zululand	Discontinuous in Africa to South Africa[52]
Linognathus setosus[1] (von Olfers)	*Alopex lagopus*[5, 52] (Linnaeus)	Canidae	Arctic fox	Worldwide[6]	Arctic regions of New World[3] and Old World
	Canis aureus Linnaeus		Indian jackal		N. Africa, S.W. Asia to Thailand, S.E. Europe
	Canis familiaris[55] Linnaeus		Domestic dog		Worldwide

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host
Order Anoplura, family Linognathidae—*Continued*					
Linognathus setosus[1] (von Olfers) ***—Continued***	*Canis latrans*[5] Say	Canidae[5]	Coyote[3]		U.S., north to Alaska; Canada to[52] Hudson Bay; Mexico; Central America to Costa Rica
	Canis lupus Linnaeus		Gray or timber wolf		Originally in North America, Europe, Asia; now eliminated from nearly all settled areas
	Canis mesomelas Schreber		Black-backed jackal		S. Africa, north to Ethiopia and Sudan
	Vulpes vulpes (Linnaeus)		Old World red fox		Palearctic region, most of Oriental region,[18] much of North America
Linognathus spicatus[1] Ferris	*Connochaetes taurinus*[52] (Burchell)	Bovidae	Blue wildebeest (brindled gnu)	South Africa: N. Transvaal[1]	Tanganyika, Kenya through N. South Africa
Linognathus stenopis (Burmeister)	*Capra hircus* Linnaeus		Domestic goat[5]	Worldwide[6]	Worldwide[6]
	Capra ibex Linnaeus		European ibex[18]		Formerly France, Switzerland, Austria, Germany; now in N. Italy[52]
	Rupicapra rupicapra (Linnaeus)		Chamois		Mtn. ranges in Europe[18] and Asia Minor
Linognathus taeniotrichus Werneck	*Cerdocyon thous*[3] (Linnaeus)	Canidae	Crab-eating fox	Brazil: Minas Gerais,[1] Ceará	South America[3, 53]
	Dusicyon culpaeus[38] (Molina)		South American fox,[53] Colpeo fox		Andes Mts.[53] in Argentina, Paraguay, and Chile
Linognathus taurotragus Bedford	*Tragelaphus oryx*[5] (Pallas)	Bovidae	Eland[3]	South Africa: Orange Free State, Natal	Subsaharan Africa[52]
Linognathus tibialis (Piaget)	*Aepyceros melampus* (Lichtenstein)		Impala	South Africa; Netherlands: Zoological Garden of Rotterdam	C. and S. Africa[16] from Kenya and Uganda to N. South Africa
	Antidorcas marsupialis (Zimmermann)		Springbok		(See above)
	Gazella dama (Pallas)		Nanger, dama		Subsaharan Africa[5]
	Gazella subgutturosa Guldenstadt		Persian gazelle		Middle East to Mongolia[18] and W. China
Linognathus tragelaphi[30] Fiedler & Stampa	*Tragelaphus scriptus*[52] (Pallas)		Bushbuck[30]	South Africa: Transvaal (Pretoria District)[30]	Most of Subsaharan Africa[16] except S.W. Africa
Linognathus vulpis[39] Werneck	*Vulpes ruepelli*[18] (Schinz)	Canidae	Sand fox[18]	Pakistan: Karāchi;[39] Iran: Khuzistan[40]	N. Africa, Arabia[18] to Pakistan
	Vulpes vulpes[5] (Linnaeus)		Old World red fox[5]		Palearctic region, most of Oriental region, much of North America

Appendix B. Hosts and distribution of lice in the order Anoplura—*Continued*

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host

Order Anoplura, family Linognathidae—*Continued*

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host
Linognathus vituli[6] (Linnaeus)	*Bos taurus* Linnaeus	Bovidae[5]	European cattle[3]	Worldwide[6]	Worldwide
	Bos indicus Linnaeus		Zebu cattle[23]		Native to India; now worldwide
Linognathus zumpti[27] Fiedler & Stampa	*Raphicerus campestris*[16] (Thunberg)		Steenbok[5]	South Africa: N.E. Transvaal;[27] Botswana; Mozambique[37]	Angola to South Africa[16] to S. Kenya
	Sylvicapra grimmia (Linnaeus)		Gray duiker[16]		Subsaharan Africa except lowlands of Zaire Basin
Solenopotes binipilosus[36] (Fahrenholz)	*Mazama gouazoubira*[36] (Fischer)	Cervidae	Gray brocket[5]	North and South America[6]	Central America:[51] Panama; to South America
	Odocoileus virginianus[5] (Zimmermann)		White-tailed deer		S. Canada, most of U.S., to N. South America
Solenopotes burmeisteri[1] (Fahrenholz)	*Cervus elaphus* Linnaeus		European red deer	N. Europe[36]	Europe to C. Asia;[18] N. Africa
Solenopotes capillatus Enderlein	*Bos taurus* Linnaeus	Bovidae	European cattle[3]	North America, Europe,[6] South Africa, Korea, Australia	Worldwide[3]
Solenopotes capreoli Freund	*Capreolus capreolus*[55] (Linnaeus)	Cervidae	Roe deer[5]	Czechoslovakia,[1] Eurasia[55]	N. Europe, N. Asia[18]
Solenopotes ferrisi (Fahrenholz)	*Cervus canadensis*[38] Erxleben (may = *C. elaphus*)		Wapiti (elk)	Probably same as hosts; may be a synonym of *S. burmeisteri*[1]	W. U.S., W. Canada
	Odocoileus hemionus Rafinesque		Mule deer		W. Canada, W. U.S.,[3] to N. Mexico
	Odocoileus hemionus[12] *columbiana* (Richardson)		Black-tailed deer		Canada: British Columbia; south to U.S.: California
	Odocoileus virginianus (Zimmermann)		White-tailed deer		S. Canada, most of U.S., to N. South America
Solenopotes muntiacus Thompson	*Muntiacus muntjac*[5] (Zimmermann)		Muntjac	Cambodia, Sri Lanka,[36] Thailand, Nepal, Taiwan	India to S. China;[52] Indochina; Indonesia: Borneo; Sri Lanka
Solenopotes natalensis[36] Ledger	*Raphicerus campestris*[52] (Thunberg)	Bovidae	Steenbok	South Africa: Natal; Mozambique	Angola to South Africa[16] to S. Kenya
Solenopotes tarandi[49] (Mjöberg)	*Rangifer tarandus* (Linnaeus)	Cervidae	Caribou, reindeer	Sweden; U.S.: Alaska[49]	Arctic regions, circumpolar region[52]
Microthoracius cameli[55] (Linnaeus)	*Camelus dromedarius*[5] Linnaeus	Camelidae[5]	Arabian camel (dromedary)[18]	Algeria[1]	Originally in Arabia;[3] now almost worldwide in domesticated state and in zooms

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host
Order Anoplura, family Microthoracidae					
Microthoracius mazzai[41, 42] Werneck	*Lama glama*[38] (Linnaeus) (questionable)		Llama[51]	U.S.: Washington, DC (National Zoological Park); Argentina: Jujuy (Santa Catalina); Bolivia: Choquecomato; Peru	Peru: Andes Mts.,[5] Bolivia and parts of Ecuador, Argentina, Chile
Microthoracius minor Werneck	*Lama glama* (Linnaeus)		Llama	Argentina, Peru[55]	(See above)
	Lama pacos[3, 38] (Linnaeus)		Alpaca		High plateaus of Peru and Bolivia[52]
Microthoracius praelongiceps (Neumann)	*Lama glama*[38] (Linnaeus)		Llama	South Africa: Zoological Garden[1, 55] of Onderstepoort; Peru; Bolivia: Choquecomato	(See above)[5]
	Lama guanicoe[52] (Muller)		Guanaco		S. Argentina: Patagonia,[53] south to Tierra del Fuego; Peru; Bolivia
Order Anoplura, family Neolinognathidae					
Neolinognathus elephantuli[1] Bedford	*Elephantulus*[52] *brachyrhynchus* (A. Smith)	Macroscelididae[5]	Short-snouted elephant shrew[43]	South Africa:[1] Onderstepoort, Transvaal; Kenya: Loita Plains	Kenya, Uganda,[52] to N. South Africa and Namibia
	Elephantulus rupestris (A. Smith)		Rock elephant shrew		South Africa: Cape Province; Namibia
	Petrodromus tetradactylus Peters		Four-toed elephant shrew		Kenya; Tanzania to Mozambique; part of S. Africa; Angola; Zanzibar
Neolinognathus praelautus Ferris	*Elephantulus rufescens*[3] (Peters)		East African long-eared elephant shrew[3]	Kenya: Lime Springs, Vor	Ethiopia, Kenya,[44] to Tanzania
Order Anoplura, family Pecaroecidae					
Pecaroecus javalii[6] Babcock & Ewing	*Tayassu tajacu*[5] (Linnaeus)	Tayassuidae[5]	Collared peccary[5]	U.S.: Arizona,[45] New Mexico, Texas	U.S.: Texas, New Mexico,[3] Arizona; to S. Argentina
Order Anoplura, family Pedicinidae					
Pedicinus albidus[1] (Rudow)	*Macaca nemestrina*[46] (Linnaeus)	Cercopithecidae[46, 52]	Pig-tailed macaque[46]	Morocco; England:[1] Zoological Garden of London	Malay Peninsula;[46] Indonesia: Sumatra, Borneo, a few adjacent islands

Louse	Host			Distribution	
	Scientific name	Family	Common name	Louse	Host
Order Anoplura, family Pedicinidae—*Continued*					
Pedicinus albidus[1] (Rudow) ***—Continued***	*Macaca sylvanus*[52] (Linnaeus)	Cercopithecidae[46, 52]	Barbary ape[46]		Morocco, Algeria,[52] introduced to Gibraltar
Pedicinus ancoratus[1] Ferris	*Procolobus verus* (Van Beneden)		Silvered leaf monkey	Indonesia: Borneo, Sumatra (Pulo Seban[55]); Malaysia; India; Pakistan: Kashmir; Sri Lanka	Burma; Indonesia: Sumatra, Java, Borneo, small adjacent islands
	Semnopithecus entellus (Dutresne)		Entellus langur		Sri Lanka; India; Nepal; China: S. Tibet; Kashmir
	Presbytis rubicunda (Müller)		Maroon leaf monkey		Indonesia: Borneo
Pedicinus badii[54] Kuhn & Ludwig	*Procolobus badius* (Kerr)		Red colobus	Probably same as host	W. equatorial Africa
	Colobus polykomos (Zimmermann)		Black-and-white colobus		Equatorial Africa
Pedicinus cercocebi Kuhn & Ludwig	*Lophocebus albigena* (Gray)		Grey-cheeked mangabey	Uganda, Congo[54]	Zaire: Kinshasa; Uganda; widespread across equatorial Africa
	Cercocebus torquatus (Kerr)		Sooty mangabey		Guinea to Ivory Coast
	Macaca mulatta (Zimmermann)		Rhesus macaque		Most of S.E. Asia
Pedicinus cynopitheci Kuhn & Ludwig	*Macaca nigra* (Desmarest)		Celebes crested macaque	U.S.: Washington, DC (National Zoological Park)	Indonesia: N. peninsula of Celebes, Halmahera (Batjan, adjacent islands)
Pedicinus eurygaster[1, 54] (Burmeister)	*Cercocebus torquatus* (Kerr)		Sooty mangabey	India; Pakistan:[1, 54] Kashmir; Malaysia; Philippines[55]	Guinea to Ivory Coast
	Cercopithecus mona (Schreber)		Mona monkey		Introduced and established in New World in West Indies: St. Kitts Island (Lesser Antilles); equatorial Africa: Ghana to Cameroon
	Cercopithecus nictitans (Linnaeus)		Greater white-nosed guenon		Equatorial Africa: Liberia to Chad
	Hylobates lar (Linnaeus)	Hylobatidae	White-handed gibbon		S.E. Asia
	Macaca cyclopis (Swinhoe)	Cercopithecidae	Formosan macaque		Taiwan
	Macaca fascicularis (Raffles)		Crab-eating macaque		Burma; India: Nicobar Islands; Thailand; Malaysia; Indonesia: Sumatra, Java, Borneo, small adjacent islands; east to Philippines

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host
Order Anoplura, family Pedicinidae—*Continued*					
Pedicinus eurygaster[1, 54] (Burmeister) —***Continued***	*Macaca mulatta*[1, 52, 55] (Zimmermann)	Cercopithecidae[52]	Rhesus macaque[46]		Most of S.E. Asia[46]
	Macaca nemestrina (Linnaeus)		Pig-tailed macaque		Malay Peninsula; Indonesia: Sumatra, Borneo, a few adjacent islands
	Macaca radiata (Geoffroy)		Bonnet monkey		S. India
	Macaca silenus (Linnaeus)		Lion-tailed macaque		S.W. India
	Macaca sinica (Linnaeus)		Toque monkey		Sri Lanka
	Papio hamadryas (Linnaeus)		Hamadryas baboon		Arabia, Egypt, Sudan, Ethiopia, Somaliland, to South Africa
	Presbytis entellus (Dufresne)		Entellus langur		Sri Lanka; India; Nepal; China: S. Tibet· Kashmir
Pedicinus ferrisi[54] Kuhn & Ludwig	*Cercopithecus aethiops* (Linnaeus)		Vervet, grivet monkey	Kenya, Rwanda, South Africa, Tanzania, Uganda, Zaire[55]	Most of Africa south of Sahara
	Cercopithecus cephus (Linnaeus)		Red-eared guenon		Cameroon to S.W. and N.W. Gabon
	Cercopithecus mitis Wolf		Diademed guenon		Ethiopia to South Africa; S. and E. Zaire; N.W. Angola
	Cercopithecus petaurista (Schreber)		Black-cheeked white-nosed monkey		C. Africa
Pedicinus hamadryas[1, 54] (Mjöberg)	*Cercopithecus aethiops*[52, 54] (Linnaeus)		Vervet, grivet monkey	Germany: Zoological Garden of Hamburg;[1] S. Africa[55]	Most of Africa south of Sahara
	Colobus abyssinicus caudatus (Linnaeus)		Abyssinian black-and-white colobus[14]		Tanzania: Mt. Kilimanjaro[16]
	Macaca sinica (Linnaeus)		Toque monkey		Sri Lanka
	Papio hamadryas[52] (Linnaeus)		Hamadryas baboon		Arabia, Egypt, Sudan,[46] Ethiopia, Somaliland, to South Africa
Pedicinus miopitheci Kuhn & Ludwig	*Miopithecus talapoin* (Schreber)			Equatorial Guinea, Gabon[55]	Angola, S.W. Zaire[52]
Pedicinus obtusus (Rudow)	*Cercocebus torquatus*[1, 52, 54, 55] (Kerr)		Vervet, grivet monkey	No specific locality; probably taken from captive animals[1]	Guinea to Gabon
	Cercopithecus diana (Linnaeus)		Diana monkey		Sierra Leone to Ghana
	Cercopithecus lhoesti Sclater		L' hoest's monkey		Cameroon: Mt. Cameroun; Equatorial Guinea: Bioko; to E. Zaire, W. Uganda, Rwanda, Burundi

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host
Order Anoplura, family Pedicinidae—*Continued*					
Pedicinus obtusus[1, 54] (Rudow) ***—Continued***	*Cercopthecus mona*[5] (Schreber)	Cercopithecidae[52]	Mona monkey[46]		(See above)[52]
	Cercopithecus nictitans (Linnaeus)		Greater white-nosed monkey		Equatorial Africa: Ghana to Cameroon
	Colobus guereza Rüppell		Black-and-white colobus monkey[5]		Senegal across C. Africa[16] to Ethiopia
	Erythrocebus patas[52] (Schreber)		Patas monkey		C. Africa: In savannahs of W. Africa to Ethiopia, Kenya, and Tanzania
	Macaca arctoides (I. Geoffroy)		Stump-tailed macaque[16]		S. China; India: Assam; Malaysia
	Macaca cyclopis (Swinhoe)		Formosan macaque		Taiwan
	Macaca fascicularis (Raffles) (includes *M. irus*)		Crab-eating macaque		(See above)
	Macaca fuscata (Blyth)		Japanese macaque		Japan[52]
	Macaca maura sp. (Schinz)		Moor macaque		Indonesia: S. Sulawesi
	Macaca mulatta (Zimmermann)		Rhesus macaque		Most of S.E. Asia
	Macaca nemestrina (Linnaeus)		Pig-tailed macaque[46]		Malay Peninsula;[46] Indonesia: Sumatra, Borneo, a few adjacent islands
	Macaca nigra (Desmarest)		Celebes crested macaque		Indonesia: peninsula of Celebes, Halmahera (Batjan, adjacent islands)
	Macaca silenus (Linnaeus)		Lion-tailed macaque		S.W. India
	Nasalis larvatus (Wurmb)		Proboscis monkey		Indonesia: Borneo
	Papio hamadryas (Linnaeus)		Hamadryas baboon		Arabia, Egypt, Sudan,[46] Ethiopia, Somaliland, to South Africa
	Procolobus verus (Van Beneden)		Silvered leaf monkey		Sierra Leone to Togo, E. Nigeria[52]
	Semnopithecus entellus (Dufresne)		Entellus langur		Sri Lanka; India; Nepal; China: S. Tibet; Kashmir
	Trachypithecus obscurus[50] (Reid)		Dusty leaf monkey		S. Thailand, Malaya, adjacent islands
Pedicinus patas[1] (Fahrenholz)	*Chlorocebus aethiops*[52] (Linnaeus)		Grass monkey[46]	Kenya,[1] Congo, Liberia, South Africa, Zaire[55]	Most of Africa south of Sahara
	Cercopithecus mitis Wolf		Diademed guenon		Ethiopia to South Africa; S. and E. Zaire; N.W. Angola

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host

Order Anoplura, family Pedicinidae—*Continued*

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host
Pedicinus patas[1] (Fahrenholz) —*Continued*	*Cercopithecus mona*[52] (Schreber)	Cercopithecidae[52]	Mona monkey[46]		(See above)
	Cercopithecus neglectus Schlegel		De Brazza's monkey		Africa: S.E. Cameroon to Uganda[13] and N. Angola; W. Kenya; S.W. Ethiopia; S. Sudan
	Erythrocebus patas (Schreber)		Patas monkey		(See above)
	Procolobus badius (Kerr)		Red colobus		W. equatorial Africa[52]
Pedicinus pictus Ferris	*Procolobus badius* (Kerr)			Kenya; England: Zoological Garden of London[1]	W. equatorial Africa[52]
	Colobus polykomos (Zimmermann)		Black-and-white colobus		Gambia to Nigeria: Benin
	Semnopithecus entellus (Dufresne)		Entellus langur		(See above)
Pedicinus veri[54] Kuhn & Ludwig	*Procolobus badius* (Kerr)		Red colobus	Liberia, Sierra Leone[54]	W. equatorial Africa
	Procolobus verus (van Beneden)		Silvered leaf monkey		Sierra Leone to Togo

Order Anoplura, family Pediculidae

Louse	Host: Scientific name	Host: Family	Host: Common name	Distribution: Louse	Distribution: Host
Pediculus humanus[1] Linnaeus (includes *P. atelophilus*, *P. chapini*, *P. lobatus*)	*Homo sapiens*[6] Linnaeus	Hominidae[6]	Humans[6]	Cosmopolitan[6]	Worldwide[6]
	Ateles spp.	Cebidae	Spider monkeys[18]		S. Mexico, Central America,[46] South America
	Hylobates syndactylus[52] (Raffles)	Hylobatidae	Siamang		Malaysia, Indonesia[46]
Pediculus mjobergi[1, 48] Ferris	*Alouatta* spp.	Cebidae	Howler monkeys		S. Mexico, Central America, South America[52]
	Ateles spp.[6]		Spider monkeys[18]	Traveling menagerie (in Germany?),[1] Central America, Argentina, Brazil, Bolivia[55]	S. Mexico, Central America, South America
Pediculus schaeffi Fahrenholz	*Pan paniscus*[47] Schwartz	Pongidae[16]	Pygmy chimpanzee[47]	Germany: Zoological Garden of Hamburg,[1] Congo, Sierra Leone, Zaire[55]	Zaire: Congo Basin[52]
	Pan troglodytes[16] (Gmelin)		Chimpanzee[16]		Equatorial Africa:[16] Senegal east through Cameroon to Congo

Louse	Host			Distribution	
	Scientific name	Family	Common name	Louse	Host
Order Anoplura, family Polyplacidae[29]					
Alenaphthirus[e] (1 sp.)	Spp. in orders Rodentia, Logomorpha, Insectivora, Primates	Sciuridae			
Ctenophthirus[e] (1 sp.)		Echimyidae			
Docophthirus[e] (1 sp.)		Tupaiidae			
Eulinognathus[e] (23 spp.)		Bathyergidae, Chinchillidae, Ctenomyidae, Dipodidae, Muridae			
Fahrenholzia[e] (13 spp.)		Heteromyidae (mainly)			
Haemodipsus[e] (6 spp.)		Leporidae			
Lemurpediculus[e] (2 spp.)		Cheirogaleidae, Megaladapidae			
Lemurphthirus[e] (3 spp.)		Galagonidae			
Neohaematopinus[e] (41 spp.)		Sciuridae, Muridae			
Phthirpediculus[e] (2 spp.)		Indridae, Lemuridae, Megaladapidae			
Polyplax[e] (76 spp.)		Abrocomidae, Muridae, Sciuridae, Soricidae			
Proenderleinellus[e] (1 sp.)		Muridae			
Sathrax[e] (1 sp.)		Tupaiidae			
Scipio[e] (4 spp.)		Petromyidae, Thryonomyidae			

[e]Some attempts have been made to revise some of these 14 genera on a regional basis, but additional work is required.

Louse	Host			Distribution	
	Scientific name	Family	Common name	Louse	Host

Order Anoplura, family Pthiridae

Louse	Host scientific name	Host family	Host common name	Louse distribution	Host distribution
Pthirus pubis[6] (Linnaeus)	*Homo sapiens*[6] Linnaeus	Hominidae[6]	Humans[6]	Cosmopolitan[6]	Worldwide[6]
Pthirus gorillae[57] Ewing	*Gorilla gorilla*[16] (Savage & Wyman)	Pongidae[57]	Gorilla[5]	Rwanda, Zaire[55]	C. Africa[52]

Order Anoplura, family Ratemiidae

Louse	Host scientific name	Host family	Host common name	Louse distribution	Host distribution
Ratemia bassoni[27] Fiedler & Stampa	*Equus burchelli*[16] (Gray)	Equidae[16]	Burchell's zebra[16]	Namibia:[27] Mariental	Sudan; Ethiopia;[16] south to South Africa: Transvaal, Zululand
Ratemia squamulatus[1] (Neumann)	*Equus asinus*[5] Linnaeus		Domestic donkey[3]	Ethiopia; Uganda;[1] Kenya: near Nairobi	Domestic donkey worldwide;[3] wild ass N.E. Africa[16]
	Equus burchelli[16] (Gray)		Burchell's zebra[16]		(See above)[16]

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